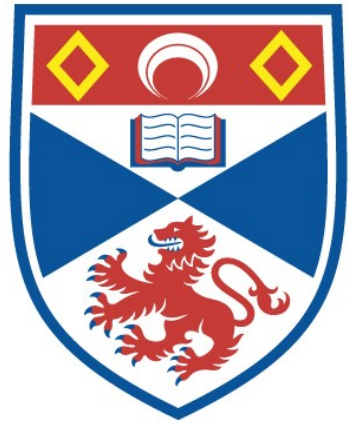
TAXONOMIC STUDIES ON GENERIC LIMITS IN THE FAMILY BORAGINACEAE, TRIBE CYNOGLOSSEAE

Robert Reid Mill

Volume II

A Thesis Submitted for the Degree of PhD
at the
University of St Andrews



1979

TAXONOMIC STUDIES ON GENERIC LIMITS IN THE FAMILY BORAGINACEAE (TRIBE CYNOGLOSSEAE)

by
ROBERT REID MILL, B.Sc.

Volume 2

TEXT
CUT OFF IN THE
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VOLUME CONTAINS CLEAR OVERLAYS

OVERLAYS HAVE BEEN SCANNED SEPERATELY AND THEN AGAIN OVER THE RELEVANT PAGE

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CHAPTER 16

8. PARACARYUM (DC.) Boiss.

16.1 INTRODUCTION

The genus Paracaryum as here delimited is the largest and most morphologically diverse in the Cynoglosseae. It comprises 69 species centred in S.W. Asia, especially from Afghanistan to Turkey, but extending W. to Greece, E. to Tibet, N. to Soviet C. Asia and S. to Sinai and Arabia (Map 16.1). In life form, its species range from perennial tufted chasmophytes and biennial herbs with large infundibular corollas, to small prostrate annuals with minute nearly rotate flowers. The nutlets, too, show an astonishing amount of diversity, particularly in ornamentation.

Although species of the genus are common constituents of the Irano-Turanian steppe, the mountains of the Lycian Taurus and Amanus in Turkey, and the Saharo-Sindian deserts, the genus has received little comparative investigation since first described and no recent monograph exists. The most recent world treatment is in fact that of BRAND (1921) and more recent accounts have tended to be confined to restricted geographical areas and have not been concerned with a critical revisionary examination of generic limits. I have studied the majority of species of both Paracaryum in the current sense and of Mattiastrum Brand, and have re-assessed the generic limits in the light of new data, as explained in sect. 16.2.

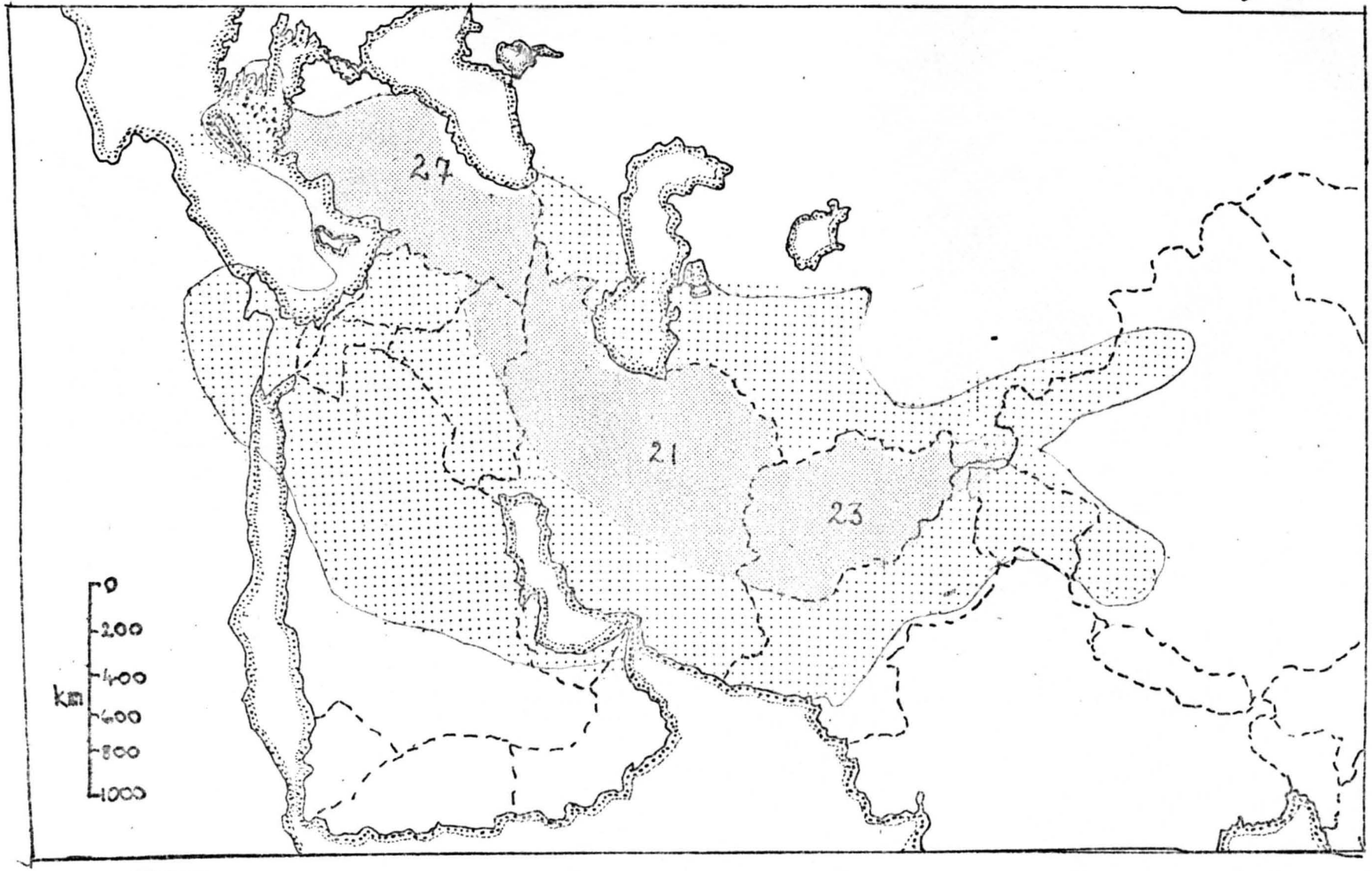
16.2 TAXONOMIC HISTORY

From the outset, Paracaryum has been a somewhat heterogeneous entity. The name was first proposed by DE CANDOLLE (1846) for one of his four sections of the genus Omphalodes Miller. Within O. sect. Paracaryum DC., he delimited two groups which were not given formal taxonomic rank but may be referred to here as 'greges':

Grex 1: calyx non accrescens nuculis maturis brevior, comprising 7 species

Map 16,1

Distribution of Paracaryum



Main centres of diversity (number of species 20 or more)

which subsequently formed part of Boissier's concept of the genus Paracaryum (BOISSIER, 1849).

Grex 2: calyx accrescens nuculis maturis longior aut eas subaequans: three species (Omphalodes linifolia (L.) Moench, O. brassicifolia (Lag.) Lehm., and O.littoralis Lehm.) currently classified in Omphalodes.

BOISSIER (1849) amalgamated Mattia Schultes sect. 3 DC. (1846) with the seven species of O. sect Paracaryum grex 1 DC. to form the genus Paracaryum (DC.) Boiss. Also included in Boissier's original concept of the genus was O. longiflora (Bentham) DC., which De Candolle had treated as a monotypic section (sect. Pseudanchusa) within his very broad concept of Omphalodes. O. longiflora is currently classified in Lindelofia (L. longiflora (Bentham) Baillon).

Boissier considered that the essential characters of Paracaryum were pendulous ovule, nutlets with flat or inflexed membranous wing and infundibular corolla with stamens included. He distinguished Paracaryum from Omphalodes by infundibular, not rotate, corolla, ovule pendulous, not straight or ascending, and different habit. From the remaining species of Mattia Schultes (now considered synonymous with Rindera Pallas) it differed by the corolla lacking a deeply laciniate limb.

Principal classifications of the Paracaryum-Mattiastrum group have been those of BOISSIER (1849, 1875); BRAND (1915, 1921); and RIEDL (1967). Limited revisions of the species inhabiting the USSR and Pakistan have been undertaken by POPOV (1953) and KAZMI (1971) respectively. For the purpose of comparison, outlines of the classifications proposed by these authors are given below. Specific names are those given by the authors and are not necessarily those currently accepted. Some species have since been reduced to synonymy or transferred to other genera.

BOISSIER (1849): The genus Paracaryum was proposed and was divided into 2 sections:

i) sect. Euparacaryum (nutlets with margin of wing introflexed, bullate,

urceolate): hirsutum, micranthum, persicum, rugulosum, undulatum.

ii) sect. Mattiastrum (nutlets flat to ± concave with ± flat wing): angustifolium, aucheri, azureum, cariense, corymbiforme, cristatum, glastifolium, lamprocarpum, leptophyllum, longiflorum, myosotoides.

BOISSIER (1875); sect. Euparacaryum was divided into 2 groups based on life form. Sect. Mattiastrum was divided into two groups on style length, the second group being further divided on the basis of corolla scale character.

Sect. Euparacaryum

Group 1 (annuals): calathicarpum, microcarpum, micranthum, salsum.

Group 2 (biennials or perennials): rugulosum, strictum, undulatum.

Sect. Mattiastrum

Group * (style 3-5 x as short as fruit): cappadocicum, cristatum, erysimifolium, lamprocarpum, leptophyllum, modestum, myosotoides, reuteri, stenolophum.

Group ** (style equalling or longer than fruit):

Subgroup X (corolla scales with apex capitate, inflated, subincurved, often retuse or bilobed): ancyritanum, asperum, aucheri, calycinum, longipes.

Subgroup X X (corolla scales tridentate with gibbous lateral teeth): angustifolium, corymbiforme, glastifolium, incanum.

BRAND (1915): the species with flat-winged nutlets were separated as the genus Mattiastrum, arguing that if classification at sectional rank within Paracaryum were to be maintained, then the genera Solenanthus and Lindelofia would have to be treated as sections of Cynoglossum. This argument, rather than a critical overall assessment of Paracaryum versus Mattiastrum, seems to have been Brand's principal reasons for the separation of Mattiastrum, which was delimited solely by the nutlet character. Within Mattiastrum, two sections were recognised, but neither was typified.

Sect. Macromattiastrum Brand (scales distinctly longer than broad): Mattiastrum ancyritanum, aucheri, calycinum, corymbiforme, erysimifolium, glastifolium, incanum, leptophyllum, longipes, racemosum, velutinum.
Sect. Modestomattiastrum Brand (scales subquadrate or broader than long; style always shorter than calyx): Mattiastrum asperum, cappadocicum, cristatum, himalayense, kurdistanicum, lamprocarpum, lithospermifolium, minutum, modestum, reuteri, sarawschanicum, stenolophum, straussii, tibeticum, turcomanicum.

BRAND (1921): Paracaryum was restricted to species having nutlets with ± incurving wing, and was not formally subdivided. P. microcarpum and P. inconspicuum were distinguished from all other species in the key by having nutlets free from the style (they are now treated as members of Lepechiniella, a genus in tribe Eritrichieae: cf. RIEDL 1963a, b, 1967). The treatment of Mattiastrum was identical to that of 1915. Two additional species (M. trinervium (Duthie) Brand and M. lambertianum (C.B. Clarke) Brand) were transferred to Mattiastrum from Paracaryum; both were included in sect. Modestomattiastrum. P. laxiflorum Trautv. and P. brachytubum Diels were doubtfully included in Paracaryum, which also comprised the following species: boissieri, bungei, calathicarpum, hirsutum, inconspicuum, intermedium, microcarpum, persicum, rugulosum, salsum, sintenisii, strictum, tenerum, thomsonii.

POPOV (1953): The genera Paracaryum and Mattiastrum were re-united. The genus was divided into 4 sections and several series, the names of which were based on Russian descriptions only and were therefore invalid under the International Code of Botanical Nomenclature.

Sect. 1 Macromattiastrum (Brand) M. Popov: incanum.

Sect. 2 Modestomattiastrum (Brand) M. Popov

series 1 Lophoptera M. Popov (wing dentate with spines): himalayense, karataviense, laxiflorum.

series 2 Holoptera M. Popov (wing entire disc of nutlet smooth): gracile, turcomanicum.

Sect. 3 Euparacaryum Boiss.: strictum.

Sect. 4 Microparacaryum M. Popov

series 1 Physodes M. Popov (wing inflated, incurving): intermedium.

series 2 Pseudo-echinospermum M. Popov (wing a narrow dentate rim): bungei.

RIEDL (1967): Paracaryum and Mattiastrum were recognised as separate genera. Paracaryum was divided into two sections, Mattiastrum into three subgenera and numerous taxa of lower rank.

Paracaryum:

Sect. Paracaryum: cyclhymonium, hirsutum, persicum, platycalyx, sintenisii, tenerum, undulatum.

Sect. Microparacaryum M. Popov ex H. Riedl: calathicarpum, intermedium, longipedicellatum, papillosum, salsum, serpentinicum, stellatum, gracile (species dubia).

Mattiastrum:

Subgen. Mattiastrum: gorganicum, luristanicum.

Subgen. Modestomattiastrum (Brand) H. Riedl

Sect. Modestomattiastrum (wing of nutlet entire or glochidiate-dentate, flat or slightly incurved). The only section: its conclusion in the taxonomic hierarchy must be considered superfluous.

Subsect. Modestomattiastrum: asperum, crista-galli, cristatum, heratense, himalayense, honigbergeri, latiflorum, modestum (type), straussii, turcomanicum.

Subsect. Caespitosa H. Riedl (tufted habit, perennials): acrocladum, densum, formosum (type), nigrum, pygmaeum, subscaposum.

Subsect. Annua H. Riedl (annual): bungei.

Exalata

Subsect. H. Riedl (wing of nutlet reduced or absent): cynoglossoides, flaviflorum, polyanthum (type).

Subgen. Mediomattiastrum H. Riedl: dielsii (type), sessiliflorum.

In this account, I follow Popov in proposing that Mattiastrum be re-united with Paracaryum. As already mentioned, Brand proposed Mattiastrum solely on the character of flat nutlet wing as compared with the incurved wing of Paracaryum sensu stricto, and supported its separation by an 'argument of logic' rather than by correlation of the nutlet character with other characters which could be used to differentiate the two taxa. Characters of the nutlet have been stressed in past studies on generic limits in Boraginaceae, and their over-emphasis has sometimes resulted in unnatural classifications (e.g. DE CANDOLLE's treatment of Omphalodes). Data from comparative studies of habit, vegetative and floral morphology as well as studies of nutlet development suggest that Brand and later workers placed too much emphasis on nutlet characters in their attempts to separate Paracaryum and Mattiastrum. Another factor which has tended to favour their separation in recent treatments is the limited number of taxa and therefore limited amount of variation seen by the respective workers. When all species are compared, the distinctions between the taxa based on nutlet and other characters break down incompletely and become blurred, so that separation as distinct genera becomes less justified.

Instead of the two rather unnatural genera presently recognised, the taxa fall naturally into three broad well-defined groups. These correspond to (i) Paracaryum sensu stricto; (ii) Mattiastrum subgenera Mattiastrum and Mediomattiastrum; (iii) Mattiastrum subgenus Modestomattiastrum. Two alternative classifications are therefore possible:

a) the separation of the three groups as three distinct genera.

b) the recognition of a single genus with three major infrageneric groups.

The latter alternative is adopted here for the following reasons:

1. Intermediates occur which link and unite the various taxa into a coherent generic entity, the unity of which is lost when the genus is split into Paracaryum and Mattiastrum, as has been done by most Western authors

since BRAND (1915). Mattiastrum subgen. Mattiastrum is distinguished from M. subgen. Modestomattiastrum by scales longer than broad, and anthers borne above bases of scales, and from Paracaryum by the above characters and by flat wing. However, P. persicum Boiss., while clearly referable to Paracaryum sensu stricto on account of inflexed wing, has scales and anthers similar to those of M. subgen. Mattiastrum. P. laxiflorum Trautv. has a flat-winged nutlet (and so was incorrectly referred to Paracaryum s. str. by BRAND, 1921) and corolla scales longer than broad with anthers borne above them, and is therefore referable to M. subgen. Mattiastrum if Riedl's classification is to be followed. The style is much shorter than the nutlet and included in the calyx, however, a feature more characteristic of M. subgen. Modestomattiastrum.

2. The existence of pairs of morphologically similar species differing principally on nutlet characters and which consequently have hitherto been classified in different genera, e.g. Mattiastrum kurdistanicum and Paracaryum sintenisii; M. bungei and P. calathicarpum; M. formosum and P. platycalyx.

3. The form of the rudimentary wing of the ovules in flower at anthesis is almost identical in taxa presently referred to the two genera. Differentiation into inflexed or spreading wing only takes place at a relatively late stage of development.

4. In taxa referable to Mattiastrum, sporadic forms may occur where an incurving wing develops, as in some forms of M. cappadocicum. Evidently, normally flat-winged taxa may possess latent genetic capability to develop an incurving wing, and vice versa (cf. SHMIDA 1978). An incurving wing may also develop at a very late stage of development (rarely collected) in Mattiastrum: in no case, however, does the wing completely curve inwards, partly enclosing the nutlet, as in Paracaryum sensu stricto.

5. The very great similarity in floral morphology between taxa currently classified in P. sect. Paracaryum and M. subgen. Modestomattiastrum suggests

that these two taxa are very closely related and may have had a common ancestor. There are no floral characters by which these taxa may be safely differentiated. Non-fruiting material is often referred to the wrong taxon (and even to Cynoglossum: see sect. 15.7) in herbaria and is sometimes unclassifiable.

6. In both genera as currently delimited, certain features of nutlet and floral morphology vary in such a way that many genes appear to be common to both taxa, and the characters are expressed in one or other of two states without intermediates (see also sect. 2.5.3). Examples include:

a) nutlet with few spines on keel only / nutlet with ± numerous spines scattered over surface of disc.

b) nutlet disc glochidiate /nutlet disc glabrous.

c) nutlet wing dentate / nutlet wing denticulate.

d) nutlet wing denticulate / nutlet wing entire.

e) anthers with bases above corolla scales / anthers with bases below corolla scales.

f) corolla scales longer than broad / corolla scales broader than long.

7. The existence of two major distinct pollen types (larger, ovoid, without constriction at equator; smaller, dumb-bell shaped, with equatorial constriction) in species of both genera.

For these reasons, the recognition of two separate genera does not seem justified. In the classification below, Mattiastrum is re-united with Paracaryum, which is divided into four subgenera, corresponding to Paracaryum s. str. together with the three subgenera of Mattiastrum recognised by RIEDL (1967). Sections are recognised in all subgenera except subgen. Mediomattiastrum, which is here considered to be monotypic.

Accepted Taxa:

P. acrocladum (Rech. fil. & H. Riedl) R. Mill

P. amani (Rech. fil.) R. Mill

P. ancyritanum Boiss.

P. artvinense R. Mill

P. asperum Stocks

P. aucheri (A.DC.) Boiss.

P. boissieri Schweinf. ex Aschers. & Schweinf.

P. bungei (Boiss.) Brand

P. calathicarpum (Stocks) Boiss.

P. calycinum Boiss. & Bal.

P. cappadocicum Boiss. & Bal.

P. carinatum H. Riedl (n.v.)

P. corymbiforme (DC. & A.DC.) Boiss.

P. crista-galli (Rech. fil. & H. Riedl) R. Mill

P. cristatum (Schreber) Boiss.

P. cyclhymenium (Boiss.) H. Riedl (n.v.)

P. cynoglossoides (Rech. fil. & H. Riedl) R. Mill

P. densum (Rech. fil. & H. Riedl) R. Mill

P. dielsii (Bornm.) R. Mill

P. erysimifolium Boiss.

P. flaviflorum (Rech. fil. & H. Riedl) R. Mill

P. formosum (Rech. fil. & H. Riedl) R. Mill

P. glochidiatum (Bunge) H. Riedl (n.v.)

P. gorganicum (H. Riedl) R. Mill (n.v.)

P. gracile Czernjak (n.v.)

P. heratense (Rech. fil. & H. Riedl) R. Kamelin

P. himalayense (Klotzsch & Garcke) C.B. Clarke

P. hirsutum (DC.) Boiss.

P. howardii (Kazmi) R. Mill

P. incanum (Ledeb.) Boiss.

P. intermedium (Fresen.) Lipsky

P. karataviense Pavl. ex M. Popov (n.v.)

P. kurdistanicum (Brand) R. Mill

P. lamprocarpum Boiss.

P. latiflorum (Rech. fil. & H. Riedl) R. Mill

P. laxiflorum Trautv.

P. leptophyllum (A.DC.) Boiss.

P. lithospermifolium (Lam.) Grande

P. longipedicellatum H. Riedl

P. longipes Boiss.

P. luristanicum Náb. (n.v.)

P. modestum Boiss. & Hausskn.

P. montbretii (H. Riedl) R. Mill

P. multicaule (Rech. fil. & H. Riedl) R. Mill

P. nigrum (H. Riedl) R. Mill

P. paphlagonicum (Bornm.) R. Mill

P. papillosum (DC.) Gürke

P. persicum (Boiss.) Boiss.

P. physodes (Bunge) H. Riedl (n.v.)

P. platycalyx Rech. fil. & H. Riedl

P. polyanthum (Rech. fil. & H. Riedl) R. Mill

P. polycarpum (Rech. fil.) R. Mill

P. pygmaeum (Rech. fil.) R. Mill

P. racemosum (Schreber) Britten

P. reuteri Boiss. & Hausskn.

P. rugulosum (DC.) Boiss.

P. salsum Boiss.

P. serpentinicum Rech. fil. & H. Riedl

P. sessiliflorum (Rech. fil. & H. Riedl) R. Mill

P. shepardii Post & Beauverd

P. sintenisii Hausskn. & Bornm.

P. stellatum H. Riedl

P. stenolophum Boiss.

P. straussii Hausskn. & Bornm.

P. strictum (C. Koch) Boiss.

P. subscaposum (Rech. fil. & H. Riedl) R. Mill

P. tenerum Bornm. (n.v.)

P. tibeticum C.B. Clarke

P. turcomanicum Bornm. & Sint.

Excluded Taxa:

Mattiastrum honigbergeri Rech. fil. in Ann. Naturh. Mus. Wien 55: 14 (1947) = Paracaryum asperum Stocks

M. lambertianum (C.B. Clarke) Brand in Engler, Pflanzenreich 78 (IV. 252): 61(1921) = Paracaryopsis lambertiana (C.B. Clarke) R. Mill (sect. 18.2)

M. minutum (Lipsky) Brand in Feddes Rep. 14: 156 (1915) = Lepechiniella minuta (Lipsky) M. Popov

M. saravschanicum (Lipsky) Brand, op. cit. 155 (1915) = Lepechiniella seravschanica (Lipsky) M. Popov

M. scabridum Rech. fil. in Ann. Naturh. Mus. Wien 58: 51 (1951) = Paracaryum racemosum (Schreber) Britten var. scabridum (Rech. fil.) R. Mill in Notes R.B.G. Edinb. 35: 304 (1977)

Paracaryum (DC.) Boiss. sect. Modestomattiastrum (Brand) M. Popov series 1 Lophoptera M.Popov in Fl. URSS 19: 594 (1953) nom. illegit. (descr. ross., sine cit. typ.) = P. subgen. Mattiastrum sect. Laxiflora R. Mill in Notes R.B.G. Edinb. 35: 304 (1977)

P. arabicum Velen. in Sitz. k. Böhm. Ges. Wuss. 11: 6 (1917)
= P. intermedium (Fresen.) Lipsky

P. azureum Boiss. & Heldr. ex Boiss., Diagn. ser. 1(11): 131 (1849)
= P. racemosum (Schreber) Britten

P. bornmuelleri Brand in Feddes Rep. 14: 149 (1915) = P. bungei (Boiss.) Brand

P. brachytubum Diels in Notes R.B.G. Edinb. 5: 168 (1912)
= Hackelia brachytuba (Diels) Johnston (tribe Eritrichieae)

P. capusii Franchet in Ann. Sci. Nat. ser. 6, 18: 218 (1884)
= Lindelofia tschimganica M.Popov ex Pazij

P. cariense (Boiss.) Boiss., Diagn. ser. 1(11): 130 (1849)
= P. lithospermifolium (Lam.) Grande subsp. cariense (Boiss.) R. Mill

P. coelestinum (Lindl.) Bentham & Hooker fil., Gen. Pl. 850 (1876)
= Paracaryopsis coelestina (Lindl.) R. Mill (sect. 18.2)

P. corymbiforme sensu Tchih., As. Min. Bot. 2: 115, t. 21 (1862) non (DC. & A.DC.) Boiss. (1849) = P. racemosum (Schreber) Britten

P. denticulatum Boiss. & Huet ex Boiss., Diagn. ser. 2(3): 174 (1856), nomen = P. cristatum (Schreber) Boiss. subsp. cristatum

P. emiri M. Popov, Descr. Pl. Turk. 66, t. 16 (1916) = P. himalayense (Klotzsch & Garcke) C.B. Clarke

P. erigerifolium Schott & Kotschy in Boiss., Diagn. ser. 2(3): 140 (1856)
= P. racemosum (Schreber) Britten

P. erythraeum Schweinf. mss. in herb. Boiss., nom. nud. = Adelocaryum erythraeum Brand

P. glastifolium (Willd.) Boiss., Diagn. ser. 1(11): 131 (1849)
= P. incanum (Ledeb.) Boiss.

P. heliocarpum Kerner, Rev. Naturw. Ver. Innsbruck 1: Suppl. 105 (1870)
= Lindelofia anchusoides (Lindl.) Lehm.

P. inconspicuum Brand in Feddes Rep. 13: 549 (1915) = Lepechiniella inconspicua (Brand) H. Riedl

P. intermedium (Fresen.) Lipsky var. papillosum (DC.) Kazmi in J. Arn. Arb. 52: 125 (1971) = P. papillosum (DC.) Gürke

P. intermedium (Fresen.) Lipsky var. stellatum (H. Riedl) Kazmi, loc. cit. (1971) = P. stellatum H. Riedl

P. lambertianum C.B. Clarke in Hooker fil., Fl. Brit. India 4: 161 (1883) = Paracaryopsis lambertiana (C.B. Clarke) R. Mill (sect. 18.2)

P. lamprocaryum (Boiss.) Walpers in Ann. Bot. 143 (1852) = P. lamprocarpum Boiss.

P. longiflorum (Bentham) Boiss., Diagn. ser. 1(11): 132 (1849) = Lindelofia longiflora (Bentham) Baillon

P. macrotrichum Vatke in Zeitschr. Ges. Nat., N.S. 11: 125 (1875) = P. modestum Boiss. & Hausskn. ex Boiss.

P. malabaricum C.B. Clarke in Hooker fil., Fl. Brit. India 4: 160 (1883) = Paracaryopsis malabarica (C.B. Clarke) R. Mill (sect. 18.2)

P. micranthum (DC.) Boiss., Diagn. ser. 1(11): 129 (1849) = P. intermedium (Fresen.) Lipsky

P. microcarpum Boiss., op. cit. ser. 2(3): 139 (1856) = Lepechiniella microcarpa (Boiss.) H. Riedl

P. minutum Lipsky in Acta Horti Petrop. 26: 488 (1910) = Lepechiniella minuta (Lipsky) M. Popov

P. myosotoides (Labill.) Boiss., op. cit. ser. 1(11): 130 (1849) = P. lithospermifolium (Lam.) Grande subsp. lithospermifolium

P. myosotoides sensu Franchet, Pl. Turkestan 218 (1884) non (Labill.) Boiss. (1849) = P. himalayense (Klotzsch & Garcke) C.B. Clarke

P. persicum (Boiss.) Boiss. var. cyclhymenium (Boiss.) Brand in Engler, Pflanzenreich 78 (IV. 252): 49 (1921) = P. cyclhymenium (Boiss.) H. Riedl

P. ponticum (C. Koch) Boiss., Pl. Or. Nov. Dec. 2: 9 (1875) = P. leptophyllum (A.DC.) Boiss.

P. rubriflorum Stocks in Hooker's J. Bot. (Kew Gard. Misc.) 4: 175 (1852) = P. rugulosum (DC.) Boiss.

P. rugulosum (DC.) Boiss. var. cyclhymenium Boiss., Fl. Or. 4: 256 (1875) = P. cyclhymenium (Boiss.) H. Riedl

P. rugulosum (DC.) Boiss. var. longistylum Bornm. in Beih. Bot. Centr. 20B: 190 (1906) = P. persicum (Boiss.) Boiss.

P. rugulosum (DC.) Boiss. p.p. min. excl. typ. = P. persicum (Boiss.) Boiss.

P. serawschanicum Lipsky in Acta Horti Petrop. 26: 488 (1910) = Lepechiniella seravschanica (Lipsky) M. Popov

P. sibthorpianum Boiss., Diagn. ser. 1(11): 130 (1849) = P. lithospermifolium (Lam.) Grande subsp. cariense (Boiss.) R. Mill

P. tenuicaule Hausskn. ex Bornm. in Beih. Bot. Centr. 20B: 191 (1906) = P. cyclhymenium (Boiss.) H. Riedl

P. thomsonii C.B. Clarke in Hooker fil., Fl. Brit. India 4: 161 (1883) = Paracynoglossum thomsonii (C.B. Clarke) R. Mill (sect. 20.2)

P. transalaicum B. Fedtsch. in Rast. Turkest. 62 (1915) = Lepechiniella transalaica (B. Fedtsch. ex) M. Popov (tribe Eritrichieae)

P. trinervium Duthie in Kew Bull. 39 (1912) = Paracynoglossum sp.

P. undulatum Boiss., Diagn. ser. 1(11): 129 (1849) = P. strictum (C. Koch) Boiss.

16.3 SYSTEMATIC TREATMENT

Paracaryum (DC.) Boiss., Diagn. ser. 1(11): 128 (1849). Syn: Omphalodes Miller sect. Paracaryum grex 1 DC., Prodr. 10: 159 (1846) et Mattia Schultes grex 3 DC., op. cit. 169 (1846) pro parte; Mattiastrum (Boiss.) Brand in Feddes Rep. 14: 150 (1915).

Perennial, biennial or annual herbs, sometimes woody at base and suffruticose, cushion-forming or ± caespitose. Stems solitary to very numerous, slender to robust, erect to prostrate, terete to slightly striate, hispid to lanate, indumentum often heteromorphic with soft adpressed hairs underlying stouter ± patent setae; setae often hooked with short patent

foot and long subadpressed main portion. Sterile rosettes present in some caespitose species, otherwise ± absent. Leaves alternate, usually relatively small (to 15 cm incl. petiole, usually much less), radical and lower cauline ± long-petiolate, upper subsessile, sessile or amplexicaul; lamina spathulate, lanceolate to linear, usually ± attenuate to obtuse at base, often narrow. Inflorescence of 1-few (rarely numerous) terminal and lateral cymes, terminal cymes often 2(-3) with central alar flower. Cymes scorpioid, dense at first, rapidly elongating and straightening in fruit in most species, bracteate in lower part or ebracteate throughout. Calyx villous, hispid, tomentose, lanate or rarely subglabrous, divided ± to base into 5 linear to lanceolate or oblong equal lobes, often accrescent and becoming stellate or reflexed in fruit. Corolla blackish, violet, blue, red, pink, yellow or white, infundibular, hypocrateriform, campanulate or subrotate, 2-20 mm; limb always distinct, lobes ± patent, shorter or longer than tube, rounded to oblong, usually ± broad and obtuse. Faucal appendages always present, always distinct scales, inserted at top of corolla tube, included (but often visible, closing throat) or exserted from tube, never exserted from corolla. Scales linear, lanceolate, triangular, trapesiform or subquadrate, rarely with two median or subterminal, lateral gibbous projections, often hamately incurved, frequently emarginate at apex and papillate. Anthers linear to ovoid, not sagittate or mucronate, included or with apices rarely exserted from corolla; base of anthers situated above or below scale bases, anthers either ± surpassing scales on long filaments (Subgen. Mattiastrum) or not (Subgen. Paracaryum and Subgen. Modestomattiastrum). Filaments subequal to or much shorter than anthers, attached near middle or to lower part of anther, inserted in corolla ± at or slightly below level of scales. Style short and included, or long and ± exserted from corolla; flat-topped. Ovules 4. Gynophore high-pyramidal. Nutlets variable in morphology, always differentiated into central disc (containing seed) and ± membranous wing (wing rarely

reduced), attached apically to gynobase by large scar occupying most of ventral surface; mature nutlets cohering to style and carrying away an awn when shed. Nutlets all similar or rarely (in some annual species) heteromorphic, 2 with broad wing and 2 with wing reduced. Dorsal surface of nutlet (disc) flat or convex, lanceolate, ovoid or kite-shaped, often with a median crest, usually spinulose (spinules often with anchor-like glochids), sometimes smooth, glabrous and ± shining, rarely ± densely covered with greyish mealy papillae interspersed with thin white glochidiate hairs (P. heratense, P. multicaule). Wing usually broad, rarely narrow and reduced (P. polyanthum, P. flaviflorum, P. cynoglossoides, P. sessiliflorum), flat (Subgenera Mattiastrum, Modestomattiastrum, Mediomattiastrum) or ± strongly incurved and partly covering disc (Subgen. Paracaryum), usually single, very rarely appearing double (P. luristanicum), its margin entire, denticulate or dentate (often deeply and coarsely toothed), unarmed, spinulose or spinulose-glochidiate; surface of wing smooth (sometimes pellucid), rarely covered in 'meal' interspersed with thin glochidiate hairs (P. heratense) or with sparse sessile glochids (P. cristatum), or bullate-rugose to -gibbous (many species of subgen. Paracaryum).

1. Wing of nutlets strongly incurved, ± partly covering disc (Subgen. Paracaryum)
   2. Corolla 4-8 mm; biennials or perennials (Sect. Paracaryum)..... Group C
   2. Corolla 1.5-3(-4) mm; annuals (Sect. Microparacaryum) ..... Group D

1. Wing of nutlets flat, not covering disc
   3. Corolla scales longer than broad, base of anthers situated above base of scales (Subgen. Mattiastrum) ..... Group A
   3. Corolla scales usually broader than long, base of anthers situated below base of scales
      4. Style 8-11 mm; corolla 11-14 mm, hypocrateriform; scales exserted (Subgen. Mediomattiastrum) ..... 16. dielsii
      4. Style 1-4 mm; corolla 2-11 mm, infundibular, campanulate to almost rotate; scales included (Subgen. Modestomattiastrum)...Group B

Group A

1. Calyx subsessile, lobes erect in fruit and surpassing nutlets; corolla lobes incurved (Sect. Sessiliflora) ..... 15. sessiliflorum

1. Calyx ± distinctly pedicellate, lobes ± spreading in fruit, much shorter than nutlets; corolla lobes not incurved

2. Wing of nutlets with double margin, outer margin incurved, inner recurved ..... 14. luristanicum

2. Wing of nutlet with single margin

3. Style shorter than or subequal to calyx

4. Nutlets 8-10 mm diam., style 4.5-6 mm at anthesis

5. Corolla blue when dry, 7.5-8.5 mm; scales with usually flat apex ..... 10. leptophyllum

5. Corolla whitish to flesh-coloured when dry, 6-6.5 mm; scales with incurved apex ..... 9. erysimifolium

4. Nutlets 5.5-6.5 mm diam., style c. 3 mm at anthesis

6. Corolla 3-3.5 mm; scales 0.6-0.9 mm, shorter than corolla lobes, broadening slightly at apex ..... 12. montbretii

6. Corolla 4.7-5.7 mm; scales c. 1.4 mm. subequal to corolla lobes, upper part sublinear, narrow ..... 11. laxiflorum

3. Style longer than calyx

7. Scales with two small lateral appendages

8. Appendages of scales subterminal, apex of scales very short, obtuse ..... 3. racemosum

8. Appendages of scales median, apex of scales long-acuminate to subulate

9. Corolla dark reddish-violet when dry; wing of nutlet usually denticulate; lower leaves 8-10(-15) mm broad ..... 1. incanum

9. Corolla pale azure when dry; wing of nutlet entire; lower leaves (11-) 15-20 mm broad ..... 2. corymbiforme

7. Scales without lateral appendages

10. Corolla tube shorter than limb ..... 4. longipes

10. Corolla tube longer than limb

11. Plant long grey-tomentose (S.W. Anatolia, E. Aegean Is.) ..... 8. aucheri

11. Plant adpressed-pilose, glabrescent below (N. & adjacent C. Anatolia)

12. Corolla 10-13 mm; style 11-15 mm ..... 5. calycinum

12. Corolla 5-8(-9) mm; style 5-13 mm

13. Style 7.8-13 mm; corolla 6-9 mm, tube not more than 2 x as long as limb ..... 6. ancyritanum

13. Style 5.5-7.2 mm; corolla 5-7 mm; tube relatively long, usually 2 x length of limb ..... 7. paphlagonicum

Group B

1. Corolla scales 1.5 x as long as broad ..... 13. gorganicum

1. Corolla scales not as above

2. Disc of nutlets glabrous

3. Wing of nutlets greatly reduced (at most 0.5 mm broad); corolla yellow or yellowish-green ..... 48. flaviflorum

3. Wing of nutlet well-developed, more than 0.5 mm broad; corolla never yellow or yellowish-green, usually blue or violet

4. Habit not tufted or pulvinate, stems usually 1-few, erect; sterile rosettes absent or few

5. Stem hairs slender, thin; corolla 5 mm; wing of nutlets slightly concave (C. Anatolia) ..... 31. stenolophum

5. Stem hairs rigid, stout; corolla 4 mm; wing of nutlet flat (Amanus, Latakia) ..... 36. lamprocarpum

4. Habit ± tufted, often strongly pulvinate or caespitose with low stems and numerous sterile rosettes

6. Corolla 6-8 mm, dark violet or blackish when dry; plant silvery-villous

7. Corolla scales 1 mm; calyx lobes 3-4 mm in flower, linear ..... 23. nigrum

7. Corolla scales 1.5 mm; calyx lobes 4-5 mm in flower, lanceolate ..... 22. karataviense

6. Corolla 4-6 mm, violet to blue when dry (not blackish); plant hirsute or pilose with ± spreading hairs, not silvery-white

8. Nutlets 6-14 mm diam.

9. Nutlets 9-14 mm diam., wing 2 mm broad or more ..... 17. turcomanicum

9. Nutlets 6-8 mm diam., wing less than 1 mm broad ..... 18. gracile

8. Nutlets 5-6 mm diam.

10. Lowest leaves long-petiolate, to 100 mm long incl. petiole, 10-12 mm broad; corolla 4 mm ..... 19. straussii

10. Lowest leaves shortly petiolate or subsessile, 20-60 x 4-8 mm; corolla 5-6 mm ..... 27. formosum

2. Disc of nutlets glochidiate or echinulate (at least on keel) or with mealy papillae

11. Margin of nutlet wing subentire, without glochids

12. Lower leaves narrowly obovate; plants sericeous-villous ..... 29. lithospermifolium subsp. cariense

12. Lower leaves ± broadly ovate; plants grey-green- to white-tomentose

13. Lower leaves with lamina 80 x 8-22 mm; nutlets 6-7 x 4-6 mm, disc with glochids only on keel ..... 32. reuteri

13. Lower leaves with lamina 20-40 x 15-20 mm; nutlets 9-11 mm diam., disc with sparse scattered glochids ..... 33. amani

11. Margin of nutlet wing glochidiate, ± toothed

14. Plant grey-tomentose or white-lanate

15. Corolla 5-6 mm; wing of nutlet distinctly denticulate ..... 34. shepardii

15. Corolla 4-4.5 mm; wing of nutlet subentire or indistinctly and remotely denticulate ..... 35. polycarpum

14. Plant canescent to villous or pilose, hairs sparse to dense, but never tomentose or lanate

16. Annuals; corolla c. 2 mm

17. Stems to 35 cm; basal leaves oblong to oblong-ovate, to 60 x 5-7 mm ..... 49. tibeticum

17. Stems 10-20 cm; basal leaves (if present) narrowly linear-lanceolate, 10-15 x 1.5-2 mm ..... 50. bungei

16. Perennials or biennials; corolla usually larger than 2 mm

18. Wing of nutlet greatly reduced, sometimes only a rim

19. Stems rigid; pedicels not or scarcely elongating in fruit, 1-2 mm ..... 47. cynoglossoides

19. Stems flexuous; pedicels greatly elongating in fruit, 2.5-6(-14) mm ..... 46. polyanthum

18. Wing of nutlet not reduced, usually broad

20. Disc of nutlets ± densely greyish mealy-papillose with thin white glochidiate hairs

21. Wing of nutlet subentire or very shortly denticulate; basal leaves (incl. petiole) c. 40 x 2-3 mm ..... 24. multicaule

21. Wing of nutlets dentate, teeth large, broad; basal leaves (incl. petiole) 80-100 x 8-12 mm ..... 42. heratense

20. Disc of nutlets not mealy-papillose, glochids (when present) not thin and hair-like

22. Wing of nutlets ± coarsely dentate

23. Corolla 6-12 mm

24. Dorsal surface of nutlet wing with sparse glochids; corolla not more than 6 mm ..... 37. cristatum

24. Dorsal surface of nutlet wing glabrous; corolla 6-12 mm

25. Pedicels 3.5-6 mm in flower, elongating to 13 mm in fruit (E. Anatolia) ..... 38. kurdistanicum

25. Pedicels 0.5-3.5 mm in flower, scarcely elongating (to 5 mm) in fruit (Afghanistan, Pakistan) ..... 39. asperum

23. Corolla 2-6 mm

26. Dorsal surface of nutlet wing with sparse scattered glochids; corolla violet ..... 37. cristatum

26. Dorsal surface of nutlet lacking glochids; corolla violet, blue or white

27. Corolla white or bluish-white in dried specimens

28. Stems 1-2, slender, 15-20 cm; basal leaves petiole 30-50 x 5-10 mm .....25. acrocladum

28. Stems usually numerous, often robust, 20-60 cm; basal leaves incl. petiole 50-90 x 5-15 mm ..... 41. himalayense

27. Corolla pink, blue or violet in dried specimens

29. Corolla 2 mm ..... 44. howardii

29. Corolla 3-4 mm

30. Corolla violet; nutlets 9-10 mm diam. ..... 40. crista-galli

30. Corolla pink or blue; nutlets 6-8 mm diam. ..... 41. himalayense

22. Wing of nutlets denticulate, teeth sometimes few and remote

31. Habit tufted, caespitose or pulvinate

32. Plant densely compact pulvinate-caespitose ..... 21. densum

32. Plant ± loosely caespitose or tufted, not forming cushions

33. Corolla 7-8 mm ..... 28. subscaposum

33. Corolla 3-6 mm

34. Corolla c. 3 mm; teeth of nutlet wing remote

(N. & C. Iran) ..... 26. pygmaeum

34. Corolla 3.7-5.5(-6) mm; teeth of nutlet wing numerous

(W. & S. Turkey) ..... 29. lithospermifolium subsp. cariense

31. Habit erect to ascending, stems few to numerous but

plants not tufted

35. Corolla tube longer than limb

36. Corolla 2.5-3 mm ..... 43. artvinense

36. Corolla 3.5-5 mm

37. Hairs of stem ± antrorsely adpressed or spreading; stems

13-24 cm; robust, corolla tube 3-5 x as long as limb

.....29. lithospermifolium subsp. cariense var. erectum

37. Hairs of stem retrorsely adpressed throughout; stems

5-15 cm, slender; corolla tube subequal to or to 2 x

as long as limb

..... 29. lithospermifolium subsp. lithospermifolium

35. Corolla tube subequal to or shorter than limb

38. Nutlets 8-10 mm ..... 30. cappadocicum

38. Nutlets 5-7 mm

39. Corolla c. 8 mm; nutlets 6-7 mm ..... 20. modestum

39. Corolla 5-6 mm; nutlets 5-6 mm ..... 45. latiflorum

Group C

1. Apices of anthers exserted from corolla

2. Nutlets 5-8 mm diam., wing not bullate-rugose ..... 51. persicum

2. Nutlets 3-4 mm diam., wing bullate-rugose ..... 52. cyclhymenium

1. Anthers entirely included in corolla

3. Calyx much accrescent in fruit; habit ± tufted,
stems many ..... 53. platycalyx

3. Calyx not or hardly accrescent in fruit; habit not tufted,
stems few or solitary

4. Nutlets 4-6(-7) mm

5. Corolla scales trapeziform; basal leaves flat-margined;
nutlet margin entire or denticulate, teeth
in 2 rows ..... 55. rugulosum

5. Corolla scales obtusely triangular; basal leaves often
with undulate margin; nutlet margin denticulate,
teeth in 3 rows ..... 56. strictum

4. Nutlets 7-8 mm

6. Nutlet disc smooth or with few spines on keel ..... 54. sintenisii

6. Nutlet disc densely aculeate

7. Corolla 7-8 mm; pedicels subequal to or slightly
longer than calyx in fruit ..... 57. hirsutum

7. Corolla 5-6 mm; pedicels much longer than
calyx in fruit ..... 58. tenerum

Group D

1. Nutlets densely greyish-papillose on outer surface ..... 61. papillosum

1. Nutlets not papillose

2. Wing smooth, pellucid, not bullate (fide RIEDL & FREITAG 1972)
..... 68. carinatum

2. Wing of nutlets bullate-gibbous or -rugose

3. Wing of nutlets densely bullate-gibbous, gibbi pluriseriate, those of outer series elongate, subacute, but the rest with their margins minutely mammilliform

4. Nutlets 4-5 mm diam.; plants shortly canescent ..... 69. calathicarpum

4. Nutlets 3 x 2-2.5 mm; plants ± long-hirsute (fide RIEDL 1969) ..... 65. glochidiatum

3. Wing of nutlets bullate-rugose or -gibbous, gibbi uniseriate, usually short

5. Stem leafy only at base; bracts absent; wing of nutlets bullate-gibbous, gibbi conical or aplanate-conical, stellately spreading ..... 62. stellatum

5. Stem leafy ± throughout but leaves few; bracts usually present, 1-3, but sometimes absent; wing of nutlets bullate-rugose or -gibbous, gibbi not stellately spreading

6. Inflorescence very lax, lowest flower very remote from others; nutlets longer than broad

7. Nutlets all similar; lowest pedicels 15-25 mm in fruit ..... 67. longipedicellatum

7. Nutlets dimorphic, 2 larger and winged, 2 smaller and with rudimentary wing; lowest pedicels c. 4 mm in fruit (fide RIEDL 1969)

8. Stems to 12 cm; leaves 10-22 mm ..... 63. physodes

8. Stems to 35 mm ..... 64. boissieri

6. Inflorescence ± dense, lowest flowers not remote from others; nutlets suborbicular

9. Nutlets 4-5 mm diam. ..... 59. salsum

9. Nutlets 2.5-3.5 mm diam.

10. Fruiting pedicels elongate; 1-3 bracts present; nutlets 3-3.5 mm diam. ..... 60. intermedium

10. Fruiting pedicels very short; bracts absent; nutlets 2.5 mm diam. ..... 66. serpentinicum

Subgen. Mattiastrum (Boiss.) R. Mill in Notes R.B.G. Edinb. 35: 303 (1977). Syn: Paracaryum (DC.) Boiss. sect. Mattiastrum Boiss. Diagn. ser. 1(11): 130 (1849); Mattiastrum (Boiss.) Brand sect. Macromattiastrum Brand in Feddes Rep. 14: 150 (1915); Paracaryum (DC.) Boiss. sect. Macromattiastrum (Brand) M. Popov in Fl. URSS 19: 550 (1953); Mattiastrum (Boiss.) Brand subgen. Mattiastrum H. Riedl, in Rech. fil., Fl. Iranica - Boraginaceae 111 (1967).

Perennials or biennials. Basal leaves usually narrowly oblong, cauline ± linear. Corolla 3-17 mm, style (3-) 5 mm or more, included in or usually exserted from calyx. Corolla scales linear to oblong-triangular, 1.5-5 x 0.5-1 mm, sometimes with lateral gibbous projections, often hamately incurved. Anther bases situated above scale bases. Wing of nutlet flat.

1. Corolla small, 4-6 mm, with tube and style included in calyx ..... Sect. Laxiflora

1. Corolla usually larger, 6-17 mm, with tube and usually also style exserted from calyx

2. Calyx lobes longer than nutlets, erect; flowers ± sessile ..... Sect. Sessiliflora

2. Calyx lobes shorter than nutlets, normally ± deflexed in fruit; flowers ± distinctly pedicellate ..... Sect. Mattiastrum

Sect. Mattiastrum

Calyx lobes shorter than nutlet, ± deflexed in fruit. Flowers ± pedicellate. Corolla 6-17 mm, tube exserted from calyx, lobes ± patent, style subequal to or longer than calyx, exserted from or included in corolla. Type: P. calycinum Boiss. & Bal. in Boiss., Diagn. ser. 2(6): 261 (1859) - lectotype, apparently first designated by RIEDL (op. cit. 111, 1967). Twelve species centred in Turkey, extending to Greece (Aegean Is.), N. Iran and Soviet Armenia.

1. P. incanum (Ledeb.) Boiss., Fl. Or. 4: 262 (1875).

2. P. corymbiforme (DC. & A.DC.) Boiss., Diagn. ser. 1(11): 131 (1849).

3. P. racemosum (Schreber) Britten in J. Bot. (London) 44: 343 (1906).

1. Plants adpressed villous; leaves tomentose to sericeous-villous on both surfaces, hairs usually lacking tuberculate base ..... var. racemosum

1. Plants glabrescent-villous; leaves glabrous above, sparsely pilose beneath, hairs with tuberculate base ..... var. scabridum

P. racemosum (Schreber) Britten var. scabridum (Rech. fil.) R. Mill in Notes R.B.G. Edinb. 35: 304 (1977). Syn: Mattiastrum scabridum Rech. fil. in Ann. Naturh. Mus. Wien 58: 51 (1951).

4. P. longipes Boiss., Diagn. ser. 2(6): 126 (1859).

5. P. calycinum Boiss. & Bal., op. cit. 125 (1859).

6. P. ancyritanum Boiss., Fl. Or. 4: 260 (1875).

7. P. paphlagonicum (Bornm.) R. Mill in Notes R.B.G. Edinb. 35: 304 (1977). Syn: Mattiastrum paphlagonicum Bornm. in Mag. Bot. Lap. 30: 69 (1903).

8. P. aucheri (A.DC.) Boiss., Diagn. ser. 1(11): 131 (1849).

9. P. erysimifolium Boiss., Fl. Or. 4: 259 (1875).

10. P. leptophyllum (A.DC.) Boiss., Diagn. ser. 1(11): 131 (1849).

11. P. gorganicum (H. Riedl) R. Mill, comb. nov. Syn: Mattiastrum gorganicum H. Riedl in Rech. fil., Fl. Iranica-Boraginaceae: 111 (1967).

12. P. luristanicum Náb. in Publ. Fac. Sci. Univ. Masaryk Brno 70: 23 (1926). Sect. Sessiliflora R. Mill, sect. nov. Syn: Mattiastrum (Boiss.) Brand subgen. Mediomattiastrum H. Riedl in Rech. fil., Fl. Iranica - Boraginaceae: 124 (1967) pro parte excl. typ.

Lobi calycis erecti, quam nuculas longiores. Pedicelli fructiferi subnulli. Corolla lobis introflexis, fornicibus ad basin loborum insertis valde bilobis subexsertis. Antherae fornices superantes. Stylus longissimus nuculis superans. Nuculae saepe ala valde reducta vel ± exalatae.

Calyx lobes erect, exceeding the nutlets. Fruits subsessile. Corolla lobes introflexed; scales attached at base of lobes, deeply bilobed, subexserted from throat. Anthers surpassing scales. Style very long, exserted

from corolla and longer than nutlets. Nutlets with often very reduced wing (wing sometimes almost lacking).

Type: 13. P. sessiliflorum (Rech. fil. & H. Riedl) R. Mill, comb. nov.

Syn: Mattiastrum sessiliflorum Rech. fil. & Riedl in Rech. fil., Fl. Iranica - Boraginaceae : 125 (1967). - Monotypic, confined to E. Afghanistan (prov. Ghazni).

Riedl (1967) included Mattiastrum sessiliflorum in M. subgen. Mediomattiastrum but commented that it deviated from the other species, not only of that subgenus but also of the whole genus, in so many characters that recognition at sectional rank might be more appropriate. He did not, however, propose a formal sectional name as he considered the species to be insufficiently known. Additional palynological evidence (see sect. 16.5) supports the separation of this species from the only other species included by Riedl in his subgenus Mediomattiastrum (i.e., M. dielsii). These data, together with the reduced nutlet wing, calyx lobes longer than the nutlets and the introflexed corolla lobes, are sufficient justification for the recognition of a new section (see also sect. 16.7.1).

Sect. Laxiflora R. Mill in Notes R.B.G. Edinb. 35: 304 (1977). Syn: P. sect. Modestomattiastrum (Brand) M. Popov series Lophoptera M. Popov in Fl. URSS 19: 594 (1953), nomen illegit., pro parte.

Corolla small, shortly campanulate, 3-6 mm, tube slightly shorter than calyx, limb shorter than or subequal to tube. Corolla scales elongate. Stamens included or slightly exserted, inserted at throat. Anthers oblong. Style short, included or scarcely exserted.

Type: P. laxiflorum Trautv. in Acta Horti Petrop. 3: 274 (1875). Two species in E. Anatolia and Transcaucasia.

14. P. laxiflorum Trautv., loc. cit. (1875).

15. P. montbretii (H. Riedl) R. Mill in Davis, Fl. Turkey 6: 290 (1979).

Syn: Mattiastrum montbretii H. Riedl in Öst. Bot. Zeitschr. 110: 520 (1963).

Subgen. Mediomattiastrum (H. Riedl) R. Mill, comb. nov. Syn: Mattiastrum (Boiss.) Brand subgen. Mediomattiastrum H. Riedl in Rech. fil., op. cit. 124 (1967) pro parte quoad typ.

Subcaespitose perennial herb. Basal leaves lanceolate, 80-160 x 6-8 mm. Calyx divided into linear lobes, lobes shorter than nutlets in fruit. Corolla blue, hypocrateriform, 8-13 mm, with narrowly cylindrical tube and broad rotate limb. Scales small, trapeziform, emarginate, exserted from corolla throat. Anthers oblong-linear, apices just reaching base of scales, filaments inserted in upper $\frac{1}{3}$ of tube. Style equalling corolla, exserted from calyx. Nutlets with broad wing.

Type: 16. P. dielsii (Bornm.) R. Mill, comb. nov. Syn: Mattiastrum dielsii Bornm. in Bot. Jahrb. 66: 236 (1934); Lindelofia stenosiphon Rech. fil. in Ann. Naturh. Mus. Wien 58: 49 (1951). - Monotypic; confined to C. & E. Afghanistan (Kabul, Bamian and Ghazni provinces).

Subgen. Modestomattiastrum (Brand) R. Mill in Notes R.B.G. Edinb. 35: 305 (1977). Syn: Mattiastrum (Boiss.) Brand sect. Modestomattiastrum Brand in Feddes Rep. 14: 152 (1915); Paracaryum (DC.) Boiss. sect. Modestomattiastrum (Brand) M. Popov in Fl. URSS 19: 593 (1953) pro parte incl. typ.; Mattiastrum (Boiss.) Brand subgen. Modestomattiastrum (Brand) H. Riedl in Rech. fil., op. cit. 112 (1967).

Perennials, biennials or annuals, sometimes caespitose or pulvinate. Basal leaves usually ± oblong, cauline linear to ovate. Corolla 2.5-12 mm, campanulate or cylindrical-campanulate to ± infundibular, scales suborbicular or ± trapeziform to subquadrate, or semilunar, normally ± broader than long, often emarginate and papillate in upper $\frac{1}{2}$, 0.2-1.5 x 0.3-1.6 mm. Anther base situated below scale base. Style very short, included, 0.4-4.5(-5) mm at anthesis, ± accrescent but not exceeding 5 mm even in fruit. Nutlets with flat wing. - 35 species, with centres of diversity in Afghanistan, Iran and Turkey (mainly S. & E. Anatolia).

1. Annuals ..... Sect. Annua

1. Perennials or biennials

2. Wing of nutlet well-developed, broad, conspicuous ..... Sect. Modestomattiastrum

2. Wing of nutlet greatly reduced, sometimes rim-like ..... Sect. Exalata

Sect. Modestomattiastrum (incl. Mattiastrum subsect. Modestomattiastrum and M. subsect. Caespitosa H. Riedl, Fl. Iranica - Boraginaceae 117, 1967).

Perennial or biennial. Corolla 2.5-12 mm. Wing of nutlet conspicuous, well-developed, broad.

Type: P. modestum Boiss. & Hausskn. ex Boiss., Pl. Or. Nov. Dec. 2: 5 (1875).

17. P. turcomanicum Bornm. & Sint. ex Bornm. in Beih. Bot. Centr. 20B: 193 (1906).

18. P. gracile Czernjak. in Feddes Rep. 27: 277 (1930) (n.v.).

19. P. straussii Hausskn. & Bornm. in Beih. Bot. Centr. 20B: 192 (1906).

20. P. modestum Boiss. & Hausskn. ex Boiss., loc. cit. (1875).

21. P. densum (Rech. fil. & H. Riedl) R. Mill, comb. nov. Syn: Mattiastrum densum Rech. fil. & H. Riedl in Öst. Bot. Zeitschr. 110: 519 (1963).

22. P. karataviense Pavl. ex M. Popov in Fl. URSS 19: 715 (1953) (n.v.).

23. P. nigrum (H. Riedl) R. Mill, comb. nov. Syn: Mattiastrum nigrum H. Riedl in Rech. fil., Fl. Iranica - Boraginaceae : 118 (1967). (Incl. Mattiastrum atrum H. Riedl, and M. atroviolaceum H. Riedl, nomina nuda in sched., hb. E).

P. nigrum is clearly allied to P. karataviense but since the type of the latter has not been seen it is not known whether the taxa are conspecific. They seem to be separated only by small differences in the size of the corolla scales. P. nigrum is endemic to E. & N.E. Afghanistan, while P. karataviense was described from N.W. Kara-Tau (Soviet C. Asia: Tien Shan).

24. P. multicaule (Rech. fil. & H. Riedl) R. Mill, comb. nov. Syn: Mattiastrum multicaule Rech. fil. & H. Riedl in Dansk. Biol. Skr. 13(4): 216 (1963).

25. P. acrocladum (Rech. fil. & H. Riedl) R. Mill, comb. nov. Syn: Mattiastrum acrocladum Rech. fil. & H. Riedl, op. cit. 206 (1963).

26. P. pygmaeum (Rech. fil.) R. Mill, comb. nov. Syn: Mattiastrum pygmaeum Rech. fil. in Ann. Naturh. Mus. Wien 58: 52 (1951).

27. P. formosum (Rech. fil. & H. Riedl) R. Mill, comb. nov. Syn: Mattiastrum formosum Rech. fil. & H. Riedl in Rech. fil. op. cit. 119 (1967).

28. P. subscaposum (Rech. fil. & H. Riedl) R. Mill, comb. nov. Syn: Mattiastrum subscaposum Rech. fil. & H. Riedl in Rech. fil., op. cit. 120 (1967).

29. P. lithospermifolium (Lam.) Grande in Bull. Orto Bot. Nap. 4: 183 (1914). This species was revised by MILL (1977, 1979).

P. lithospermifolium (Lam.) Grande subsp. cariense (Boiss.) R. Mill, op. cit. 307 (1977).

- - var. cariense. Syn: Omphalodes cariensis Boiss., Diagn. ser. 1(4): 41 (1844); Paracaryum cariense (Boiss.) Boiss., Diagn. ser. 1(11): 130 (1849); P. myosotoides (Labill.) Boiss., loc. cit. (1849) pro parte excl. typ. quoad plantas turcicas, creticas.

Tufted, 5-18 cm. Stem hairs antrorsely adpressed at least above. Corolla scales tube shorter than or subequal to limb, limb not lobed at base; lobes (0.6-)1.6-1.9 x 2 mm; scales 0.5-1 x 1.1-1.4 mm

Syntypes: (Turkey, prov. Denizli) in pinguibus regionis alpinae Cadmi Orientalis (Honaz Da.), vi 1842, Boissier (G); in Caria interiori, 1842, Pinard (G).

var. erectum R. Mill, loc. cit. (1977).

Differs from var. cariense by erect habit, with few, taller, very hispid stems; limb of corolla often divided at base. Erect herb 13-24 cm tall, very hispid, setae patent. Corolla tube 3-5 x as long as limb; lobes 0.6 mm. Nutlets 0.9 mm diam.

Type: Turkey, prov. Maraş: Akher Dagh (Ahir Da.), 790 m, 2 vi 1934, Balls (holo. E, iso. K).

subsp. lithospermifolium. Syn: Cynoglossum lithospermifolium Lam., Encycl. 2: 238 (1786); C. myosotoides Labill., Icon. Pl. Syr. Rar. 2: 6, t. 20 (1791); Mattiastrum lithospermifolium (Lam.) Brand in Feddes Rep. 14: 155 (1915) pro parte incl. typ.

Stem indumentum retrorsely adpressed throughout. Corolla tube subequal to or longer than limb; limb lobed ± to base, lobes 1.1-2 x 1.2-1.6 mm. Corolla scales 0.8-1.2 x 0.6-1(-1.2) mm.

30. P. cappadocicum Boiss. & Bal. in Boiss., Diagn. ser. 2(6): 124 (1859).

31. P. stenolophum Boiss., loc. cit. (1859).

32. P. reuteri Boiss. & Haussk. in Boiss., Fl. Or. Nov. Dec. 2: 6 (1875).

33. P. amani (Rech. fil.) R. Mill in Notes R.B.G. Edinb. 35: 305 (1977).
Syn: Mattiastrum amani Rech. fil. in Ann. Naturh. Mus. Wien 58: 50 (1951).

34. P. shepardii Post & Beauv. in Dinsmore, Pl. Postianae et Dinsmorianae 1: 8 (1932).

35. P. polycarpum (Rech. fil.) R. Mill in Notes R.B.G. Edinb. 35: 308 (1977).

36. P. lamprocarpum Boiss., Diagn. ser. 1(11): 131 (1849).

37. P. cristatum (Schreber) Boiss., loc. cit. (1849).

1. Pedicels 4-13 mm in fruit; corolla scales (0.4-) 0.6-0.7 x (0.7-) 0.9-1.3 mm; nutlets (8-)9-12.5 x 7-10 mm, disc sparsely and shortly glochidiate ..... subsp. carduchorum

1. Pedicels 1.5-4 mm in fruit; corolla scales 0.4-0.5 x 0.7-1 mm; nutlets 8-10.5 x 6.5-9.5 mm, disc densely long-glochidiate ..... subsp. cristatum

subsp. carduchorum R. Mill in Notes R.B.G. Edinb. 35: 306 (1977).
Differs from subsp. cristatum by corolla limb longer than tube, larger scales, disc of nutlet with sparse scattered short glochids. Biennial, stem hirsute, hairs usually short and sparse. Leaves often pale yellowish-green in sicco. Pedicels 2.3-6 mm in flower, elongating to 4-13 mm in fruit. Scales (0.4-)0.6-0.7 x (0.7-)0.9-1.3 mm. Nutlets (8-)9-12.5 x 7-10 mm, disc sparsely and shortly glochidiate; wing with obtuse (more rarely acute) teeth; style (1.6-) 2.8-4.5 mm in fruit, ± ventricose below the capitate stigma.

Type: Turkey, prov. Hakkari: Nehil Çayi 48-55 km from Hakkari to Yüksekova, igneous slopes, 1600-1700 m, 14 vi 1966, Davis 44889 (holo. E, iso. K).

38. P. kurdistanicum (Brand) R. Mill in Notes R.B.G. Edinb. 35: 306 (1977). Syn: Mattiastrum kurdistanicum Brand in Feddes Rep. 14: 154 (1915).

39. P. asperum Stocks in Hooker's J. Bot. (Kew Gard. Misc.) 4: 175 (1852). (Incl. Mattiastrum honigbergeri Rech. fil. in Ann. Naturh. Mus. Wien 55: 14, 1947).

40. P. crista-galli (Rech. fil. & H. Riedl) R. Mill, comb. nov. Syn: Mattiastrum crista-galli Rech. fil. & H. Riedl in Dansk. Biol. Skr. 13(4): 207 (1963).

41. P. heratense (Rech. fil. & H. Riedl) R. Kamelin in Byull. Mosk. Obshch. Isp. Prirod., Biol. 80(6): 90 (1976).

42. P. himalayense (Klotzsch & Garcke) C.B. Clarke in Hooker fil., Fl. Brit. India 4: 161 (1885).

1. Biennial; stems solitary, slender, branches relatively few, not divaricate ..... var. himalayense

1. Perennial; stems robust, many, much-branched, branches divaricate ..... var. fallax

var. fallax (Rech. fil. & H. Riedl) R. Mill, comb. nov. Syn: Mattiastrum himalayense (Klotzsch & Garcke) Brand subsp. fallax Rech. fil. & H. Riedl in Rech. fil., op. cit. 117 (1967); M. himalayense (Klotzsch & Garcke) Brand var. fallax (Rech. fil. & H. Riedl) Kazmi in J. Arn. Arb. 52: 128 (1971).

43. P. artvinense R. Mill in Notes R.B.G. Edinb. 35: 305 (1977).

44. P. howardii (Kazmi) R. Mill, comb. nov. Syn: Mattiastrum howardii Kazmi in J. Arn. Arb. 52: 129 (1971).

45. P. latiflorum (Rech. fil. & H. Riedl) R. Mill, comb. nov. Syn: Mattiastrum latiflorum Rech. fil. & H. Riedl in Dansk. Biol. Skr. 13(4): 214 (1963).

Sect. Exalata (H. Riedl) R. Mill, comb. et stat. nov. Syn: Mattiastrum (Boiss.) Brand subgen. Modestomattiastrum (Brand) H. Riedl sect. Modestomattiastrum subsect. Exalata H. Riedl in Rech. fil., Fl. Iranica - Boraginaceae 122 (1967).

Perennial or biennial herbs, several to many-stemmed, but not caespitose. Inflorescence ebracteate. Corolla 2.5-4 mm, dull blue or yellowish; tube shorter or longer than calyx. Scales inserted in throat, trapeziform. Style 1-2 mm. Nutlets 2-5 mm, wing greatly reduced (sometimes to a rim), not more than 0.8 mm broad.

Type: P. polyanthum (Rech. fil. & H. Riedl) R. Mill.

Three species in C., E. & S.E. Afghanistan.

46. P. polyanthum (Rech. fil. & H. Riedl) R. Mill, comb. nov. Syn: Mattiastrum polyanthum Rech. fil. & H. Riedl in Rech. fil., op. cit. 123 (1967).

46. P. flaviflorum (Rech. fil. & H. Riedl) R. Mill, comb. nov. Syn: Mattiastrum flaviflorum Rech. fil. & H. Riedl in Rech. fil., op. cit. 122 (1967).

48. P. cynoglossoides (Rech. fil. & H. Riedl) R. Mill, comb. nov.
Syn: Mattiastrum cynoglossoides Rech. fil. & H. Riedl in Rech. fil., op. cit. 123 (1967).

Sect. Annua (H. Riedl) R. Mill, comb. et stat. nov. Syn: Mattiastrum (Boiss.) Brand subgen. Modestomattiastrum (Brand) H. Riedl sect. Modestomattiastrum subsect. Annua H. Riedl in Rech. fil., op. cit. 121 (1967).

Type: P. tibeticum C.B. Clarke in Hooker fil., Fl. Brit. India 4: 162 (1883). - Two species extending from Iran to Tibet.

49. P. tibeticum C.B. Clarke, loc. cit. (1883), incl. Mattiastrum tibeticum (C.B. Clarke) Brand var. schlagintweitii Brand in Engler, Pflanzenreich 78 (IV. 252): 66 (1921).

50. P. bungei (Boiss.) Brand in Engler, Pflanzenreich 78 (IV. 252): 47 (1921).

Subgen. Paracaryum

Perennials, biennials or annuals. Basal leaves ± oblong, cauline elliptic, narrowly oblong to linear. Corolla 1.5-8 mm, campanulate,

cylindrical-campanulate to infundibular, dark violet to blue. Scales ± trapeziform, subquadrate to semilunar, ± broader than long. Anthers usually included, their bases below the scale bases, rarely slightly exserted from corolla and then with their bases situated slightly above the scale bases (P. persicum, P. cyclhymenium). Style usually very short, sometimes subequal to calyx, 0.5-3 mm. Wing of nutlets strongly incurved, partly covering disc, often bullate-gibbous or -rugose.

1. Biennial or perennial; corolla 4-8 mm, dark violet to blue; nutlets 5-8 mm, never heteromorphic ..... Sect. Paracaryum

1. Annual; corolla 1.5-3 mm, always bright sky blue; nutlets 2-5 mm, often heteromorphic ..... Sect. Microparacaryum

Sect. Paracaryum.

Type: P. rugulosum (DC.) Boiss., Diagn. ser. 1(11): 129 (1849). - 8 species mainly in E. Anatolia, Transcaucasia and Iran.

51. P. persicum (Boiss.) Boiss., Diagn. ser. 1(11): 129 (1849).

52. P. cyclhymenium (Boiss.) H. Riedl in Rech. fil., Fl. Iranica - Boraginaceae 102 (1967).

53. P. platycalyx Rech. fil. & H. Riedl in Öst. Bot. Zeitschr. 110: 535 (1963).

54. P. sintenisii Hausskn. & Bornm. in Beih. Bot. Centr. 20B: 191 (1906).

55. P. rugulosum (DC.) Boiss., loc. cit. (1849).

56. P. strictum (C. Koch) Boiss., Fl. Or. 4: 256 (1875) pro parte excl. typ. P. hirsuti.

57. P. hirsutum (DC.) Boiss., Diagn. ser. 1(11): 130 (1849).

58. P. tenerum Bornm., Beih. Bot. Centr. 23B: 175 (1915).

Sect. Microparacaryum [M. Popov in Fl. URSS 19: 602, 1953, nom. illegit.] ex H. Riedl in Rech. fil., Fl. Iranica - Boraginaceae 104 (1967).

Lectotype: (Riedl, loc. cit., 1967): P. intermedium (Fresen.) Lipsky in Acta Horti Petrop. 26: 487 (1910). - 11 species, mainly centred in the drier parts of Afghanistan, Pakistan and Iran; P. intermedium extends from Egypt to the Tien-Shan and Baluchistan.

The taxa of this section are all very closely related and differ only in small characters, mainly of the nutlet. P. stellatum H. Riedl and P. papillosum (DC.) Gürke were reduced to varieties of P. intermedium by KAZMI (1971). I have seen insufficient material to assess the complete range of variation and therefore recognise all taxa at specific rank. The section needs monographic treatment, possibly with collateral cultivation in order to test the stability of the variation shown in the field (cf. SHMIDA 1978).

59. P. salsum Boiss., Fl. Or. 4: 255 (1875).

60. P. intermedium (Fresen.) Lipsky, loc. cit. (1910).

61. P. papillosum (DC.) Gürke in Engler & Prantl, Nat. Pflanzenfam. 4(3a): 105 (1895).

62. P. stellatum H. Riedl in Rech. fil., op. cit. 104 (1967).

63. P. physodes (Bunge) H. Riedl in Öst. Akad. Wiss. Math.-Nat. Kl. Anz. 106 (1-14): 9 (1969) - (n.v.).

64. P. boissieri Schweinf. ex Aschers. & Schweinf. in Mem. Inst. Egypt 2: 768 (1889).

65. P. glochidiatum (Bunge) H. Riedl, op. cit. 8 (1969) (n.v.).

66. P. serpentinicum Rech. fil. & H. Riedl in Rech. fil., op. cit. 107 (1967).

67. P. longipedicellatum H. Riedl in Rech. fil. op. cit. 107 (1967).

68. P. carinatum H. Riedl in Öst. Bot. Zeitschr. 120: 139 (1972).

69. P. calathicarpum (Stocks) Boiss., Fl. Or. 4: 254 (1875).

16.4 MORPHOLOGY

16.4.1 Rootstock:

The life form may be perennial, biennial or annual. Perennial and biennial species are found in all four subgenera, but annuals are restricted to subgen. Paracaryum sect. Microparacaryum and subgen. Modestomattiastrum sect. Annua.

The occurrence of caespitose and non-caespitose perennial species has attracted attention and RIEDL (1967) grouped all the Iranian and Afghan caespitose species together as Mattiastrum subgen. Modestomattiastrum subsect. Caespitosa. However, caespitose habit appears to have developed independently more than once (probably several times), as when the species of Riedl's subsect. Caespitosa are examined, they are found to differ significantly in floral, nutlet and palynological characters. P. acrocladum, for example, is only scarcely caespitose and on other grounds seems more closely allied to the P. himalayense group than to any other species of subsect. Caespitosa. P. subscaposum has a very distinctive long-tubed corolla and dumb-bell shaped pollen, both of which are characters not found in any other species of subsect. Caespitosa which I have examined. Thus, if the group is to be recognised, these two species must be excluded from it.

If a caespitose group is to be recognised within subgen. Modestomattiastrum, it would have to include not only the remaining Irano-Afghan species (P. multicaule, P. formosum, P. pygmaeum, P. nigrum, P. karataviense and P. densum) but also the Anatolian complex of caespitose species centred in the Amanus and including P. lithospermifolium, P. polycarpum, P. amani, P. reuteri and P. shepardii. These species are rather similar in their floral and pollen morphology to the above-mentioned Irano-Afghan species (especially P. formosum). However, for the reasons advanced below, I prefer to reject Riedl's subsect. Caespitosa since the Turkish taxa, which are very closely allied to each other, almost certainly arose independently from the Irano-Afghan ones and the taxon would therefore be polyphyletic. None of the Anatolian species extend into the 'Flora Iranica' area, nor do any of the Irano-Afghan taxa extend further west than N. Iran (P. pygmaeum) - the majority are centred in Afghanistan. The relationships between them are weaker and the diversity greater than between the species in the Anatolian complex. Furthermore, several species, not included by Riedl in subsect. Caespitosa, are subcaespitose, e.g. P. asperum, and it is very difficult

to draw a line between them. Moreover, there are cross-relationships between the Irano-Afghan group and P. platycalyx, a caespitose member of subgen. Paracaryum, while the nearest allies of the Anatolian complex are the non-caespitose biennials P. lamprocarpum. P. cappadocicum and P. stenolophum. Non-caespitose or subcaespitose relatives of the Irano-Afghan group are P. straussii and P. modestum. Within the Irano-Afghan group, P. densum is exceptional in forming very dense suffruticose pulvinate cushions. The other species are looser in habit, although P. pygmaeum is dwarf and suffruticose. In subgen. Mattiastrum the caespitose habit reaches its greatest development in P. racemosum; the other perennial species are subcaespitose or non-caespitose.

Non-caespitose perennials include P. sessiliflorum, P. gorganicum, P. incanum and P. aucheri of subgen. Mattiastrum; P. modestum, P. turcomanicum, P. heratense, P. latiflorum and some forms of P. himalayense in subgen. Modestomattiastrum sect. Modestomattiastrum; all three species of sect. Exalata; and P. rugulosum, P. persicum and P. sintenisii of subgen. Paracaryum. Most other species, except P. tibeticum, P. bungei and P. sect. Microparacaryum, are biennial; some normally perennial species, e.g. P. rugulosum and P. flaviflorum, may also sometimes be biennial.

Within the genus there is a progressive trend towards reduction of the rootstock correlated with change in life form. In the perennials, especially the caespitose ones, the rootstock is large, many-crowned, and deep. In the biennials there is a gradual tendency towards a less stout, shorter but still substantial stock (as in subgen. Mattiastrum) and eventually toward a thin vertical rootstock as in the P. himalayense group of species. The annuals have very slender rootstocks but as they grow in desert habitats the roots often extend deep into the substrate in search of water.

16.4.2 Stems:

Paracaryum is a genus of relatively low plants, the stems usually in the range 10-60 cm and rarely exceeding 75 cm. The stems may be fairly

stout in some species of subgen. Mattiastrum (e.g. P. incanum), but much less than in Solenanthus, and in most species they are fairly slender. The most delicate stems occur in P. gracile and the annual species.

The stems are erect to ascending in all the perennial and biennial species, and in most of the annuals, but are prostrate on some forms of P. bungei. Numerous stems are developed by many of the perennial species (even when not caespitose) but most biennials develop only 1-3 stems. Conversely, most of the annuals develop clumps of several to many thin stems, e.g. P. intermedium.

Stem indumentum is very variable. No species is completely glabrous*, although in some (e.g. P. lamprocarpum) it is glabrescent later, and in others (e.g. P. straussii) it is glabrous in the lower part with hairs confined to the upper part and inflorescence. The quality of the indumentum varies from densely adpressed canescent hairs (e.g. P. incanum) to ± long spreading setules as in P. hirsutum, P. asperum, P. modestum and P. lamprocarpum. Taxonomically, subgenus Mattiastrum is characterised largely by an adpressed sericeous, villous or tomentose indumentum, although patent hairs occur in the three Irano-Afghan species of this subgenus (P. sessiliflorum, P. gorganicum and P. luristanicum). Subgenus Modestomattiastrum shows considerable variation. The Turkish caespitose species (P. lithospermifolium group) are normally densely adpressed-sericeous to tomentose or lanate, but even within P. lithospermifolium the variation is considerable, some gatherings being silky, others (referred to subsp. cariense var. erectum) are patent-hispid like the biennial species P. cappadocicum.

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* Mattiastrum glastifolium (Willd.) Brand was described by BRAND (1921) as having glabrous stems. I know this taxon only from a microfiche of the type and only known specimen (Hb. B-Willd.). It seems to be an aberrant form of P. incanum.

The truly caespitose Irano-Afghan species are all white-hispid with a variable mixture of adpressed and subpatent hairs; P. subscaposum is distinct in having unequal patent setules which arise from tuberculate bases. The biennial species, both in Turkey and in Iran and Afghanistan, tend to have a harshly hispid indumentum of patent setules, as in P. asperum, P. heratense, P. himalayense, P. cristatum etc. Similar patent setules prevail in the perennial and biennial species of subgen. Paracaryum, but the hairs of the annual species (sect. Microparacaryum) are mainly antrorsely adpressed.

16.4.3 Leaves:

Radical and cauline leaves are present in all species of Paracaryum, although the radical leaves frequently do not persist until flowering in many biennial species, and the cauline leaves are often few and remote. Often the upper cauline leaves are reduced and bract-like as in some species of Rindera, and the upper part of the stem is completely leafless in some species, especially of subgen. Mattiastrum.

Considering the large size of the genus, there is far less variation in leaf shape compared with other genera. The total variation is from lanceolate to linear-spathulate. The radical leaves (and usually the lower cauline) are ± long-petiolate, although in a few species (e.g. P. formosum) the petiole is reduced. The lamina is always very attenuate so that the boundary between lamina and petiole is difficult to define. The cauline leaves may be amplexicaul, as in P. polycarpum, P. amani and P. shepardii.

Leaf indumentum is even more variable than that of the stem. Indumentum may be either tomentose, lanate or adpressed with dense grey or white hairs not arising from tuberculate bases (e.g. P. amani, P. lithospermifolium, P. multicaule, P. nigrum, P. incanum), or of ± sparser patent rigid setules which arise from multicellular tuberculate bases (e.g. P. asperum, P. hirsutum, P. heratense). Adpressed indumentum seems to be correlated with perennial

habit and/or a montane environment, while patent setules are found in biennial, often weedy species of open steppe habitats. Within a given species there is normally little variation in indumentum over its geographical range, although some species are notably polymorphic, P. lithospermifolium showing one of the largest ranges of variation which seems to defy classification beyond the subspecific level. In other species, well marked subspecies or varieties can be distinguished on the basis of leaf indumentum, e.g. P. racemosum vars. racemosum and scabridum, P. cristatum subspp. cristatum and carduchorum.

The leaf margin is always entire as in other genera of Cynoglosseae, but/at least three species - P. cristatum, P. subscaposum and P. strictum - it is frequently undulate.

16.4.4 Inflorescence:

Two broad types of inflorescence occur in Paracaryum. Subgenus Mattiastrum (excluding P. laxiflorum, P. montbretii and P. sessiliflorum) is characterised by a terminal pseudo-umbellate corymbose inflorescence of 2-4 scorpioid cymes arising from the same point. This type of inflorescence is similar to that of Rindera, some species of Solenanthus, Cynoglossum magellense and C. holosericeum, and on account of the similarity in inflorescence many species of this subgenus were classified in Rindera by early authors. Sometimes one or several lateral cymes are also present, as in P. calycinum.

The second type of inflorescence, variants of which are found throughout the rest of the genus, is a usually forked (2-3-geminate) terminal inflorescence often with one to several lateral cymes immediately below, and which elongate very greatly in fruit. The occurrence of this type of inflorescence in P. laxiflorum, P. montbretii and P. sessiliflorum provides one of the several links between subgenera Mattiastrum and Modestomattiastrum. The same type of inflorescence is also common in Cynoglossum and Paracynoglossum .

Table 16.1

Inflorescence Types in the Genus Paracaryum

(Groups of related species are separated by dotted lines)

Inflorescence Type	Species
Terminal pseudocorymb	incanum, corymbiforme, racemosum, calycinum, ancyritanum, paphlagonicum, erysimifolium, longipes, aucheri, leptophyllum, luristanicum.
Elongating cymes; infl. 2-3-geminate; forks short, ± divaricate	laxiflorum, montbretii
	lithospermifolium, reuteri, amani, polycarpum, shepardii, stenolophum, cappadocicum, lamprocarpum.
	multicaule, formosum, karataviense, nigrum.
	subscaposum.
	cristatum, asperum, kurdistanicum, heratense, acrocladum.
	persicum, cyclhymenium.
	rugulosum, strictum, sintenisii, hirsutum, platycalyx.
Elongating cymes; infl. 2-3-geminate; forks long, suberect	dielsii.
	crista-galli.
	himalayense, artvinense, howardii, tibeticum.
	polyanthum, flaviflorum.
Elongating cymes; infl. a single cyme, many-flowered	sessiliflorum.
	modestum, straussii.
	latiflorum, cynoglossoides.
	bungei, salsum, intermedium, longipedicellatum, stellatum, serpentinicum, boissieri, calathicarpum.
Elongating cymes; infl. a single cyme, few-flowered	gorganicum.
	turcomanicum, gracile.
	densum, pygmaeum.

The inflorescence is frequently only cursorily described in floras and has never, to my knowledge, had any taxonomic importance attached to it. Species may be grouped together, however, using the form of the inflorescence as in Table 16.1 and some quite natural groups of species are obtained by this means. All the perennial caespitose species except P. pygmaeum and P. densum have 2-3-geminate inflorescences with relatively short divaricate forks which are normally shorter than the height of the vegetative portion. The few-flowered single cymes of P. turcomanicum, P. gracile, P. densum and P. pygmaeum have no doubt been derived from this type by reduction. Of the biennials, many have 2-3-geminate inflorescences with divaricate forks and also show relationships with the biennials in other characters. P. heratense also falls within this category but is transitional to a group of five species (P. crista-galli and the P. himalayense group) having long suberect forked cymes which are frequently longer than the vegetative portion when fruiting. This group of species appears to be fairly natural (see sect. 16.7.1). P. polyanthum and P. flaviflorum in sect. Exalata have a similar type of inflorescence but in P. cynoglossoides and in P. latiflorum (sect. Modestomattiastrum) one of the forks is normally suppressed, as in most specimens of the annual species (sect. Microparacaryum).

16.4.6 Calyx:

The calyx is very variable in shape and size. From sect. Mattiastrum to sect. Microparacaryum there is a gradual trend from oblong or linear to ovate lobes, and from large to very small size. In subgen. Mattiastrum sect. Mattiastrum the lobes are consistently linear or linear-oblong. Within the section there is a reduction in length, correlated with a similar reduction in corolla size, from 10 mm or more (P. incanum, P. corymbiforme) to 4-5 mm (P. aucheri, P. erysimifolium, P. paphlagonicum). This trend is continued in sect. Sessiliflora (4-5.5 mm) and sect. Laxiflora (2 mm in flowering specimens of P. montbretii). In sect. Sessiliflora the lobes

are linear, as in sect. Mattiastrum, but the species is unique in that they remain erect in fruit and are longer than the enclosed nutlets. In sect. Laxiflora the lobes are ovate to lanceolate, as in most species of subgenera Paracaryum and Modestomattiastrum.

P. dielsii, which alone constitutes subgen. Mediomattiastrum, has 4-5 mm long linear lobes divided to the base, thus suggesting a relationship with subgenus Mattiastrum.

Within subgenus Modestomattiastrum the largest calyces are those of P. turcomanicum (5-6 mm) and P. modestum (4-7 mm). In the rest of the subgenus the lobes are narrowly lanceolate to ovate and there is a trend from lobes medium size, 3-4 mm long (P. lithospermifolium and allies, P. cristatum group, P. formosum and its relatives, P. straussii) to very small, ovate to narrowly lanceolate lobes 1-2 mm long (e.g. P. himalayense group, P. heratense, P. crista-galli, P. pygmaeum, P. flaviflorum).

The perennial and biennial species of subgen. Paracaryum show parallel trends to those of subgen. Modestomattiastrum. The largest calyces are those of P. persicum (c. 6 mm), which provides a link with subgen. Mattiastrum. In most other species of sect. Paracaryum the calyx is 3-4 mm, while in the annual species (sect. Microparacaryum and P. bungei and P. tibeticum of subgen. Modestomattiastrum) the calyx is reduced to 1-1.5 (-2) mm.

All the above measurements refer to the calyx in the flowering state. Accrescence in fruit is variable, from 20% in subgen. Mattiastrum to up to 100% in many species of the other subgenera; in a few species, such as P. acrocladum, there is no accrescence at all.

Calyx indumentum is variable but is normally similar to that of the leaves. Adpressed-strigillose calyces are commonest in subgenus Mattiastrum although in P. incanum the lobes are white-tomentose. Tomentose calyces also occur in the P. amani-P. polycarpum group in the Amanus Mts., and in the P. nigrum-P. karataviense group of Afghanistan and Tien Shan. Adpressed

indumenta are common in the P. lithospermifolium group, P. heratense and P. himalayense but in most other species the hairs are ± patent and are often setulose, arising from multicellular tuberculate bases (e.g. P. cristatum, P. asperum, P. modestum, P. strictum, P. hirsutum). Similar patent (though usually more slender) hairs occur in sect. Microparacaryum.

16.4.7 Corolla:

Although very variable in colour, shape and size, a study of the corolla in Paracaryum reveals several definite trends:

1. Size.

The largest corollas are those of subgenus Mattiastrum. In P. incanum, P. racemosum and P. corymbiforme the corollas may reach nearly 20 mm. Those of the P. calycinum group are smaller and there is a subtrend from P. calycinum (10-13 mm) through P. ancyritanum and P. leptophyllum (6-9 mm) to P. erysimifolium, P. paphlagonicum and P. gorganicum (5-7 mm). The corollas of P. sessiliflorum measure 8-9 mm, while those of P. laxiflorum (4-6 mm) and P. montbretii (3-4 mm) are the smallest in the subgenus and comparable in size to many species of subgenera Modestomattiastrum and Paracaryum.

The corollas of P. dielsii measure 13-15 mm and are thus similar in size to the P. incanum-racemosum group of subgenus Mattiastrum.

In subgenus Modestomattiastrum the largest corollas examined are those of P. kurdistanicum and P. asperum, typically 9-12 mm. Some forms of P. asperum have smaller corollas 5-8 mm long and have been named Mattiastrum honigbergeri Rech. fil., but the range in variation is continous and I follow KAZMI (1971) in treating the taxa as synonymous. P. modestum and the P. nigrum-karataviense group also have relatively large corollas at 6-8 mm, but in most species they are smaller. Corollas 4-6 mm are common in many perennial species and their biennial derivatives, e.g. P. lithospermifolium and its relatives, P. cristatum, P. straussii, P. latiflorum, P. subscaposum, and P. formosum. Smaller ones 3-4 mm long prevail in the P. himalayense

Figure 16.1

(Drawings 1-10 are of opened-out corollas, x 4.4;

drawings 1a-10a are of faucal scales, x 8.7 approx.)

1, 1a *P. incanum* (T. Baytop ISTE 12731)

2, 2a *P. racemosum* (Tobey 2150)

3, 3a *P. calycinum* (Tobey 2454A)

4, 4a *P. ancyritanum* (T. Baytop ISTE 13393)

5, 5a *P. paphlagonicum* (Bornmüller 14414)

6, 6a *P. aucheri* (Davis 1707)

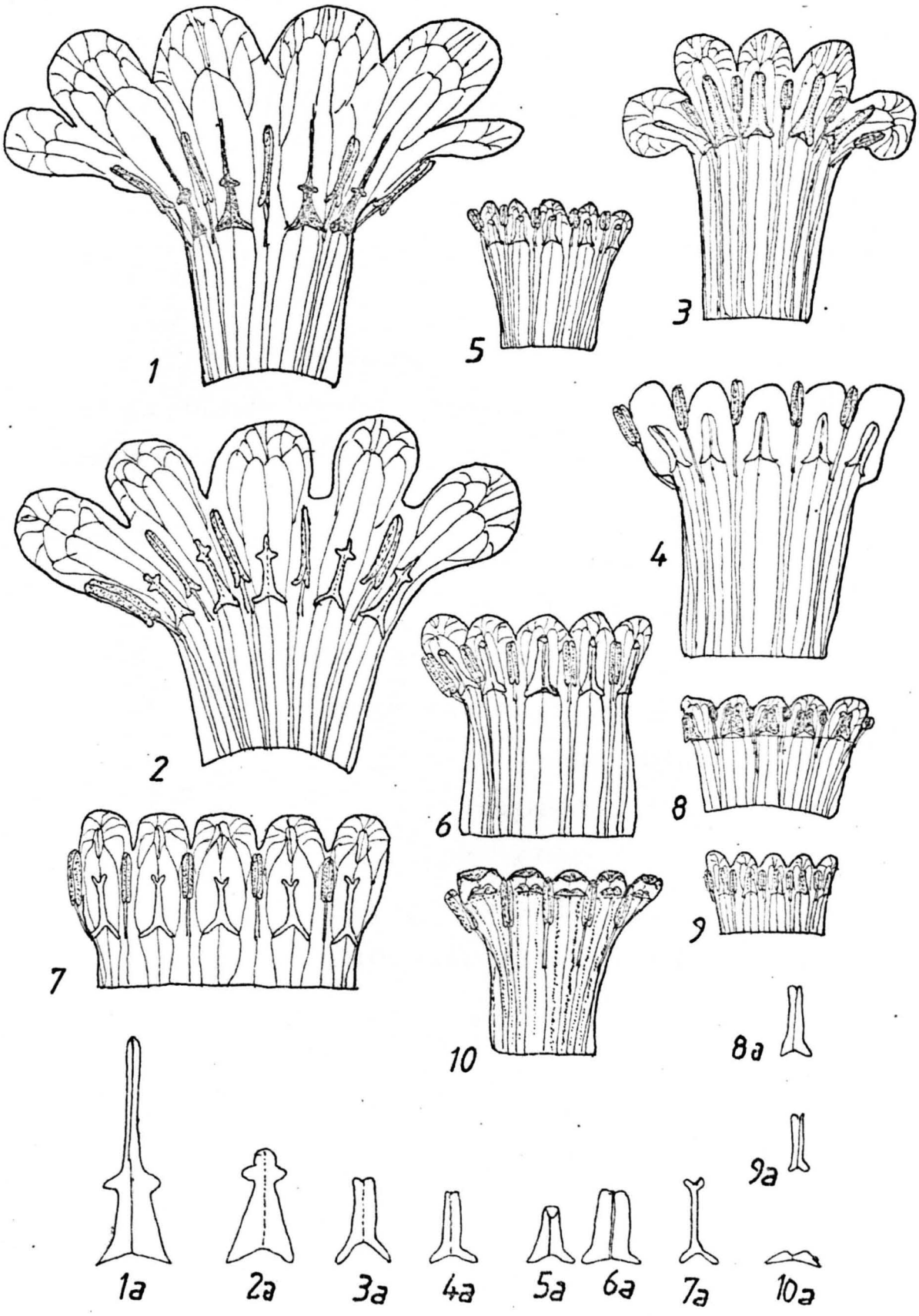
7, 7a *P. longipes* (Siehe 378)

8, 8a *P. laxiflorum* (Davis 30826)

9, 9a *P. montbretii* (Montbret 2544)

10, 10a *P. sessiliflorum* (Rechinger 17385)

Figure 16,1



group, including P. artvinense which has the smallest corollas of any Turkish species. In sect. Exalata, P. cynoglossoides has the largest corollas (4-5 mm), while P. flaviflorum has the smallest (2.5-3 mm).

The biennial and perennial species of subgen. Paracaryum have corollas similar in size to their relatives in subgen. Modestomattiastrum, P. platycalyx having the largest (10-11 mm), and most species having 3-6 mm corollas e.g. P. rugulosum and P. hirsutum. The annual species of sect. Microparacaryum have the smallest corollas of the genus (1.5-3 mm).

2. Shape:

There is a gradual trend throughout the genus from infundibular to subrotate corollas, with reduction in the tube.

Subgenus Mattiastrum (Fig. 16.1) is characterised by infundibular corollas with the tube normally longer than the limb. The tube usually expands slightly near the throat, particularly in P. racemosum (ic. cit., no. 2), P. incanum (no. 1) and P. corymbiforme, but tends to be subcylindrical in some species of the P. calycinum group (nos. 3-7). Even in this subgenus the beginning of the trend towards a campanulate corolla can be detected, but the tube remains longer than the limb, even in sect. Laxiflora (nos. 8, 9).

Only four species outwith subgen. Mattiastrum normally have corolla tubes markedly (more than 2 x) longer than the limb. These are P. dielsii (subgen. Mediomattiastrum: Fig. 16.2, no. 1), P. subscaposum (of isolated taxonomic position within the subgen. Modestomattiastrum: Fig. 16.2, no. 7), and P. persicum (Fig. 16.2, no. 5) and P. cyclhymenium of subgen. Paracaryum. Certain other species occasionally have long-tubed variants, e.g. P. lithospermifolium subsp. cariense var. erectum, while in the P. himalayense group and P. turcomanicum (Fig. 16.2, no. 2) the tube is usually slightly longer than the limb. In most other species the corolla is campanulate and the limb and tube are subequal, but P. densum, P. straussii and P. modestum (Fig. 16.2, no. 16) have subrotate corollas with very short tubes, similar to Omphalodes. The annual species of sect. Microparacaryum show a trend

Figure 16.2

Paracaryum subgenera Mediomattiastrum and Modestomattiastrum: Floral Morphology

(All drawings are of opened-out corollas, 4.4 x natural size)

1 P. dielsii (Hedge & Wendelbo W. 5030)

2 P. turcomanicum (Sintenis 103)

3 P. lithospermifolium (Wood & Gibson 191)

4 P. multicaule (Hedge & Wendelbo W.7194)

5 P. reuteri (Davis 20203)

6 P. cappadocicum (Huber-Morath 11550)

7 P. subscaposum (Lindberg 969)

8 P. formosum (Rechinger 31422)

9 P. pygmaeum (Rechinger 6022)

10 P. nigrum (Hedge & Wendelbo W.5430)

11 P. acrocladum (Edelberg 1451)

12 P. cristatum (Davis 47382)

13 P. asperum (Hedge & Wendelbo W.2728)

14 P. heratense (Köie 3937)

15 P. crista-galli (Rechinger 4502)

16 P. modestum (Morton 3770)

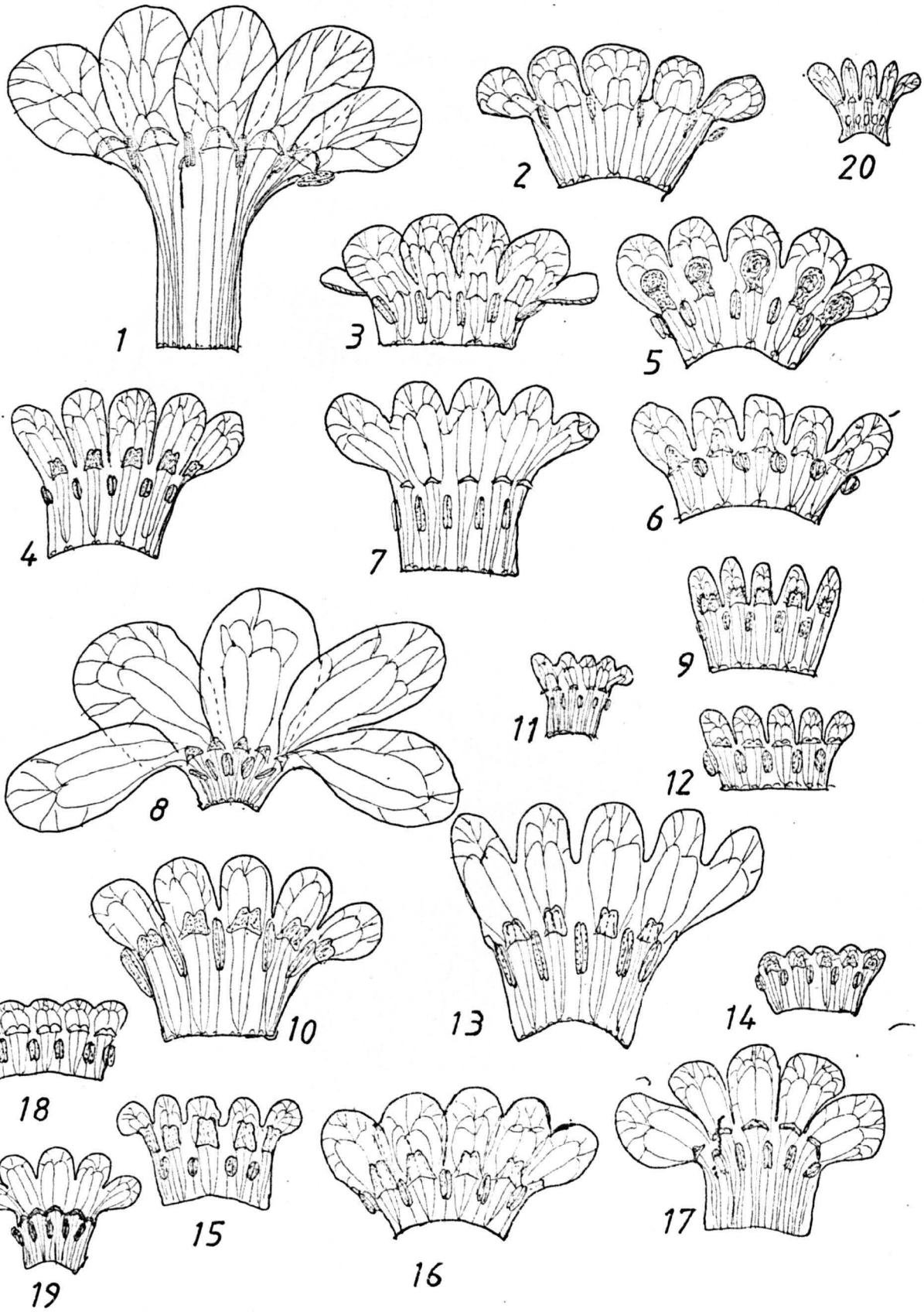
17 P. latiflorum (Köie 2641)

18 P. flaviflorum (Hedge & Wendelbo W4781)

19 P. polyanthum (Rechinger 17688a)

20 P. bungei (Lamond 681)

Figure 16,2



from campanulate corollas with the tube slightly longer than the limb (P. intermedium: Fig. 16.3, no. 10) or subequal to it (P. boissieri: Fig. 16.3, no. 7) to corollas with the tube usually slightly shorter than the limb (P. calathicarpum, P. stellatum: Fig. 16.3, nos. 8 & 9). In these annual species, corolla tube length appears to show variation; the corolla of P. calathicarpum illustrated has a tube which is rather unusually long for the species.

3. Faucal scales:

The genus shows considerable variety in the form of the faucal appendages, but the prevailing trend is a change from large linear scales to small triangular ones.

Subgenus Mattiastrum (Fig. 16.1, nos. 1a-10a) is characterised by the corolla scales oblong to linear, longer than broad. This character is specific for the subgenus and for P. persicum and P. cyclhymenium of subgen. Paracaryum. Within subgen. Mattiastrum two sub-groups can be distinguished:

a. Scales linear, with two lateral gibbous appendages separating the apical and basal portions (P. racemosum, P. incanum, P. corymbiforme).

b. Scales oblong or lingulate to subtriangular, lacking lateral appendages (all other species).

The species in the first group can be further subdivided according to the position of the lateral appendages. In P. corymbiforme and P. incanum (Fig. 16.1, no. 1a) the scales are long (4-5 mm) with median appendages and a very narrow subulate apical portion. In P. racemosum (2a) the appendages are subterminal and the shorter (1-2 mm) scales somewhat resemble those of Lindelofia anchusoides and its allies. This type of scale represents an intermediate between those of the P. incanum group and those of the rest of the subgenus, which have probably been derived by further shortening together with loss of the appendages.

The second group can be divided according to whether the scales have

a flat or involute apex. Although some species, notably P. ancyritanum, (4a) show variation, those with larger corollas normally have flat scales (P. leptophyllum, P. calycinum: 3a) while those with small corollas have involute scales (P. erysimifolium, P. aucheri (6a), P. paphlagonicum (5a)). P. longipes (7a) is unique in having linear scales which broaden apically, the apex being truncate or even retuse. P. sessiliflorum, P. gorganicum and P. luristanicum also have bilobed scales. In the latter two species they are lingulate as in other members of the subgenus (fide RIEDL 1967), but P. sessiliflorum (10a) is unique in the subgenus in having very low, small semilunar scales, inserted at the base of the lobes, not in the corolla throat as in all other species. This, together with the numerous other distinctive features of the species (introflexed corolla lobes, nutlets almost wingless and shorter than erect calyx lobes, etc.), suggests that the species deserves sectional rank (cf. sect. 16.3). Both species of sect. Laxiflora agree with the rest of subgen. Mattiastrum in having oblong-linear scales.

Except for P. cyclhymenium and some specimens of P. persicum, oblong-linear scales do not occur in subgenera Paracaryum, Modestomattiastrum or Mediomattiastrum, although P. nigrum (Fig. 16.2, no. 10) and P. karataviense show a slight tendency towards the oblong outline; these species also have the largest scales in these subgenera (1 mm long or more). In the perennial species the scales are usually subquadrate or trapeziform, and very frequently emarginate.

Subquadrate, emarginate scales are also found in biennials related to perennials, e.g. P. cappadocicum (Fig. 16.2, no. 6). In P. latiflorum (Fig. 16.2, no. 17), P. subscaposum (Fig. 16.2, no. 7) and some species of the P. himalayense group, e.g. P. acrocladum (Fig. 16.2, no. 11) there is a tendency for the scales to become relatively shorter and broader, becoming low-triangular or semilunar; this is also the case in sect. Microparacaryum (Fig. 16.3, nos. 7-10). The scales of P. dielsii are exserted from the

Figure 16.3

Paracaryum subgenera Modestomattiastrum and Paracaryum:

Floral Morphology

(All drawings are of opened out corollas; 1-5, 7-10 x 8.7, 6, x 4.4)

1 P. cynoglossoides (Rechinger 17688b)

2 P. strictum (Stainton 8283)

3 P. hirsutum (Davis 28623)

4 P. sintenisii (Davis 28907)

5 P. persicum (Edmondson & Miller 1652)

6 P. platycalyx (Lamond 713)

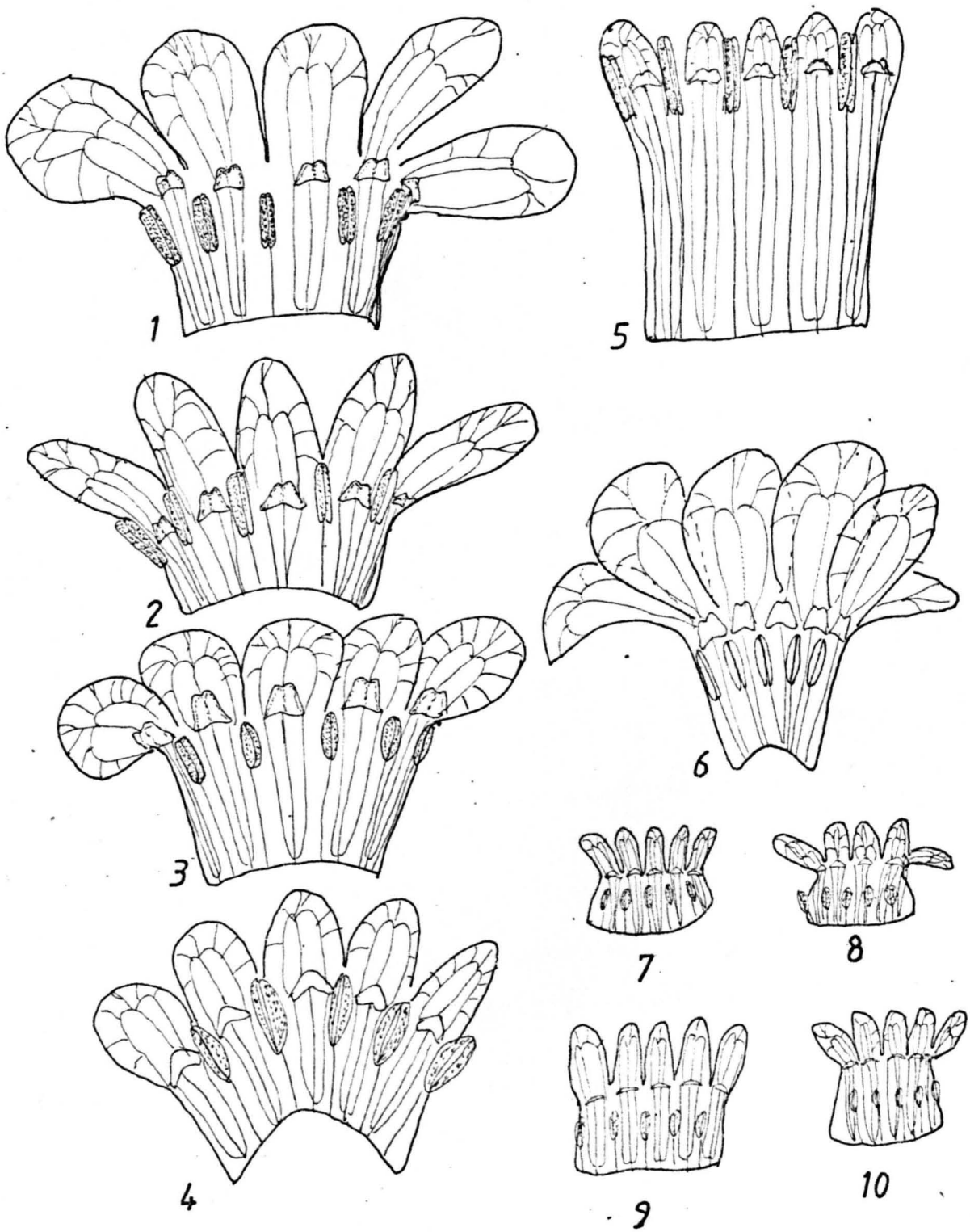
7 P. boissieri (Davis 6794)

8 P. calathicarpum (Rechinger 36238)

9 P. stellatum (Rechinger 33428)

10 P. intermedium (Koelz 11853)

Figure 16,3



corolla throat - a condition which is unique in the genus.

4. Stamens:

The stamens in Paracaryum are inserted either in the throat or in the middle of the tube; filaments may be long or very short, and the anthers may be borne either above or below the scale bases.

All species of subgenus Mattiastrum have stamens with relatively long filaments and oblong anthers borne above the scale bases. No species of subgen. Modestomattiastrum has this combination of characters, and in subgen. Paracaryum it is confined to P. persicum and P. cyclhymenium.

In subgen. Mattiastrum, there is a tendency for the anthers to become smaller and more ovoid with decreasing corolla size. The largest, most linear anthers, measuring 2-4 x 0.4-0.5 mm, are those of P. incanum, P. corymbiforme and P. racemosum. In the species of the P. calycinum group these is a gradual decrease in anther size from c. 2.5 x 0.6 mm in P. ancyritanum to c. 1.3 x 0.5 mm in P. aucheri, while those of P. sessiliflorum, P. laxiflorum and P. montbretii are still smaller (c. 1 mm long). In P. sessiliflorum the anthers only just exceed the scales, and thus their position is intermediate between those typical of subgenera Mattiastrum and Modestomattiastrum.

In subgenus Modestomattiastrum the stamens are inserted in the middle or upper half of the tube. Although their apices slightly surpass the scale bases in some species (e.g. P. asperum and P. flaviflorum) most of the anther always lies below them. (The same is true of P. dielsii). The largest, most linear anthers in subgen. Modestomattiastrum are those of P. nigrum, P. karataviense and P. asperum. In most perennial and biennial species of both subgenera Modestomattiastrum and Paracaryum the anthers are oblong-ovoid, attached so that their apices reach or just exceed the base of the scales. P. artvinense also has this type of anther attachment and so is transitional to the other members of the P. himalayense

group (including P. himalayense, P. heratense and P. howardii), all of which have very small ovoid or broadly ovoid anthers, the apices of which do not usually reach the scale bases. P. bungei and all members of sect. Microparacaryum have minute ovoid anthers positioned in the middle of the tube well below the corolla scales.

5. Style:

Style length is also useful for distinguishing subgenera. Subgenus Mattiastrum is characterised by long styles, normally exceeding the calyx and frequently equalling or longer than the corolla, as in P. incanum. The subgenus shows a trend towards reduction in style length, however, and in several species it is included in the calyx, although still longer than is typical of subgen. Modestomattiastrum. P. laxiflorum and P. montbretii have still shorter styles, similar in length to those of subgen. Modestomattiastrum.

In the other subgenera the style is always included in the calyx and frequently much shorter than it. The trend towards a very short style, begun in subgen. Mattiastrum, is continued, and is part of the general change from relatively large to very small corollas with smaller, more ovoid anthers.

6. Corolla colour:

The predominant corolla colour in Paracaryum is blue or violet, but P. flaviflorum has yellowish corollas, while those of P. nigrum and P. karataviense are dark blackish maroon. Other unusual colours are those of P. erysimifolium (flesh coloured), P. polyanthum (greyish blue) and P. incanum (deep wine red).

Apart from P. erysimifolium, P. incanum, P. corymbiforme (pale azure) and P. racemosum (brilliant ultramarine), most species of subgenus Mattiastrum have violet or blue-violet corollas. Intensely violet or brownish-violet corollas also prevail in the P. lithospermifolium group, the P. cristatum-asperum group and several other species of subgenus

Modestomattiastrum, and in all the perennial and biennial species of subgenus Paracaryum. The corollas of P. modestum and P. straussii are deep blue, and the P. himalayense group is characterised by sky-blue to whitish-blue flowers. All the annual species have vivid to sky blue corollas.

16.4.8 Nutlets (Figures 16.4-16.7):

The nutlets of Paracaryum resemble those of Rindera, and differ from those of Cynoglossum, in the presence of a broad ± membranous wing. Two distinct types of wing occur in Paracaryum, flat and incurved, and these were used by BRAND (1915) to delimit the two genera Paracaryum sensu stricto and Mattiastrum. Intermediates with slightly incurving wings do occur in some species, however, and partly for this reason I prefer to recognise one broad genus (cf. sect. 16.2).

The flat type of nutlet wing occurs throughout subgenera Mattiastrum, Modestomattiastrum and in P. dielsii. The wing is reduced in P. sessiliflorum and practically absent in sect. Exalata, but in most species it is broad and well developed. Its margin may be entire, coarsely dentate or minutely denticulate. Species having similar nutlet wings are often closely related in other characters, e.g. P. cristatum (Fig. 16.6, nos. 6-7), P. kurdistanicum (Fig. 16.6, no. 8) and P. asperum (Fig. 16.6, no. 9) (cristate or repand-dentate), P. lithospermifolium (Fig. 16.5, no. 7), P. cappadocicum (Fig. 16.5, no. 8), P. amani, P. shepardii (Fig. 16.5, no. 10) P. reuteri (Fig. 16.5, no. 11) and P. stenolophum (Fig. 16.5, no. 9) (wing ± minutely denticulate, tending to be subentire or entire).

In subgenus Paracaryum the whole wing incurves strongly to partly enclose the dorsal surface of the nutlet. The outer surface of the wing in this subgenus is frequently bullate, rugose or gibbous, and its rim may be entire or may bear up to 3 rows of gibbous teeth. Smooth or muricate wing surfaces prevail in sect. Paracaryum (except P. cyclhymenium which is bullate-rugose), while bullate nutlets are more common in sect. Microparacaryum (Fig. 16.7, nos. 9-15). Technical characters of the wing

Figure 16.4

Paracaryum subgen. Mattiastrum: Nutlet Morphology

1 P. incanum, x 3.5 (Bornmüller 14407)

2 P. racemosum, x 3.5 (Davis 19147)

3 P. calycinum, x 3.5 (Sorger 71-63-5)

4 P. ancyritanum, x 3.5 (Davis 38049)

5 P. aucheri, x 3.5 (Peşmen & Aydar EGE 12517)

6 P. longipes, x 3.5 (Siehe 507)

7 P. paphlagonicum, x 3.5 (Bornmüller 14414)

8 P. laxiflorum, x 3.5 (Davis 30826)

9 P. sessiliflorum, x 3.5 (Rechinger 17385)

10 P. sessiliflorum, calyx and nutlet, x 10 (Rechinger 17385)

11 P. montbretii, x 3.5 (Montbret 2544)

Figure 16,4

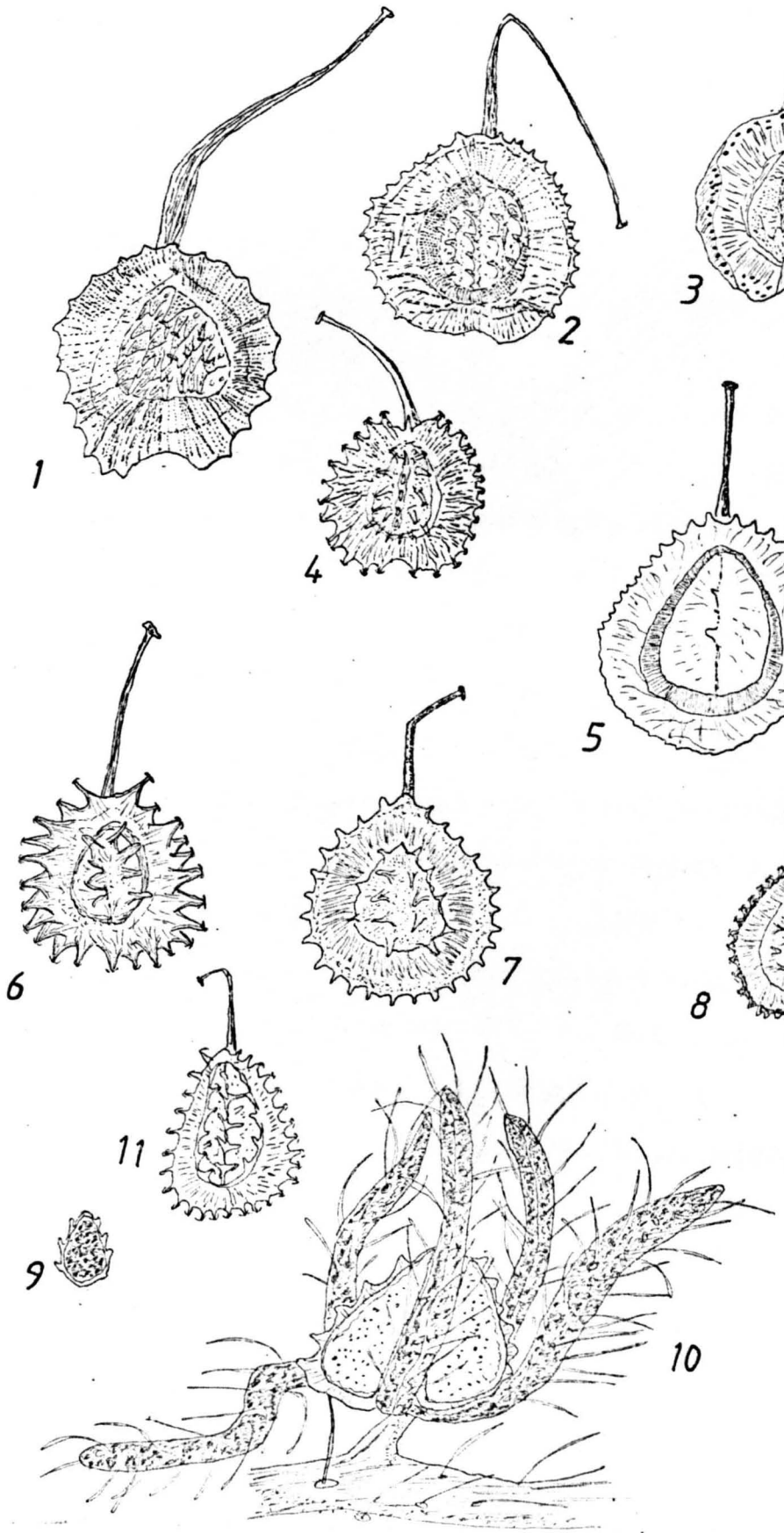


Figure 16.5

Paracaryum subgenera Mediomattiastrum and Modestomattiastrum:

Nutlet Morphology

1 P. dielsii, x 4.4 (Hedge & Wendelbo W.4299)

2 P. turcomanicum, x 4.4 (Phrandkeviy s.n.)

3 P. multicaule, x 4.4 (Lindberg 380/1958): 3a marginal glochid, x c. 85 3b glochid on surface of disc, x c. 85 3c glochid on surface of wing, x c. 85

4 P. acrocladum, x 8.7 (Ekberg 1451)

5 P. formosum, x 4.4 (Rechinger 31422)

6 P. subscaposum, x 4.4 (Lindberg 969/1960)

7 P. lithospermifolium, x 4.4 (Davis 9772) 7a glochids on margin of wing, x c. 85

8 P. cappadocicum, x 4.4 (Huber-Morath 11550) 8a glochids on margin of wing, x c. 85

9 P. stenolophum, x 4.4 (Peşmen 1050)

10 P. shepardii, x 4.4 (Akman 281)

11 P. reuteri, x 4.4 (Davis 20282)

Figure 16,5

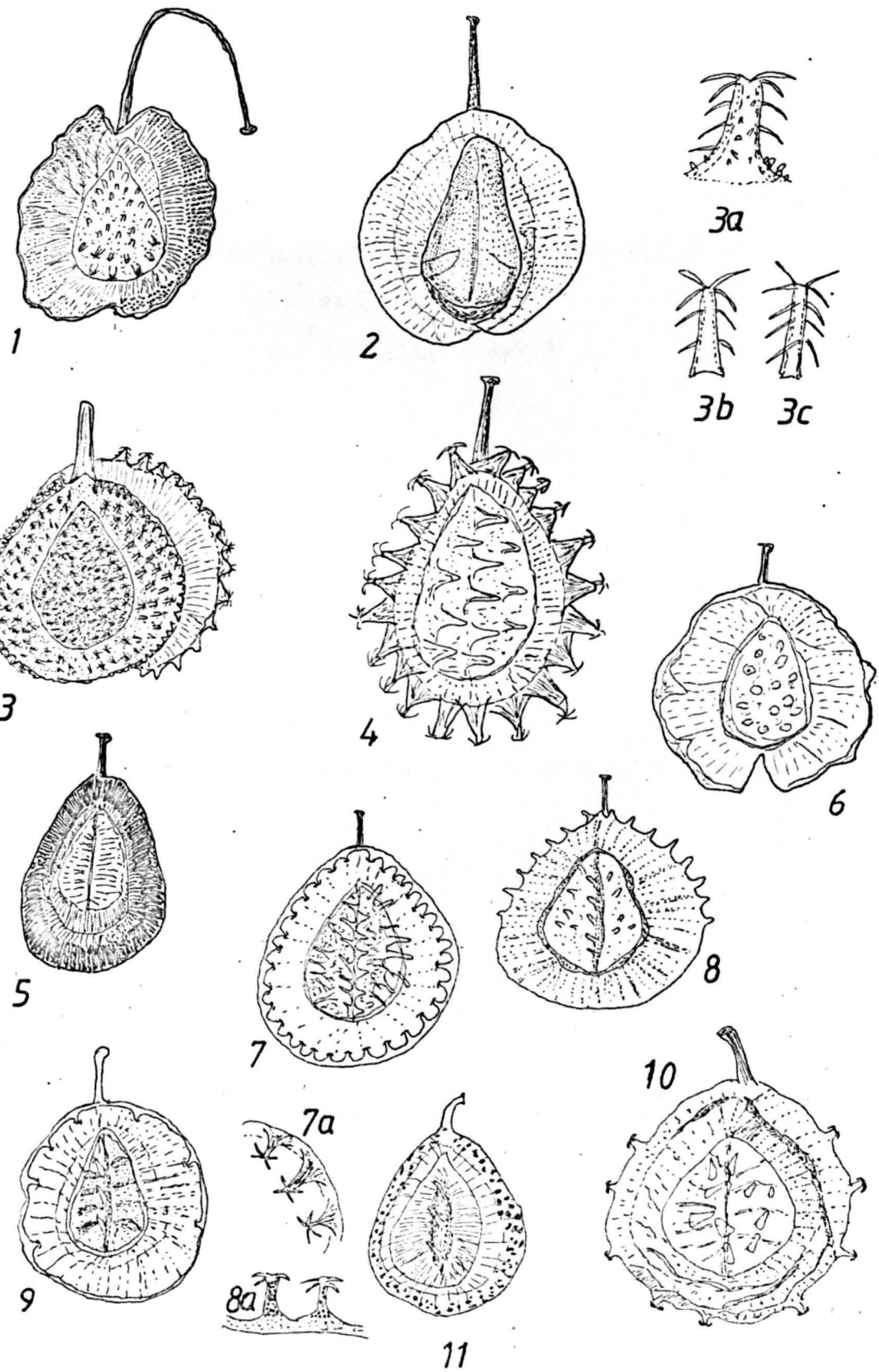


Figure 16.6

Paracaryum subgen. Modestomattiastrum: Nutlet Morphology (ii)

1 P. polycarpum, x 4.4 (Stainton & Henderson 5650)

2 P. lamprocarpum, x 4.4 (Davis 6178a)

3 P. artvinense, x 4.4 (Davis 30085)

4 P. pygmaeum, x 4.4 (Rechinger 6022)

5 P. densum, x 4.4 (Rechinger 12800)

6 P. cristatum subsp. cristatum, x 4.4 (Davis 47382)

7 P. cristatum subsp. carduchorum, x 4.4 (Davis 44889)

8 P. kurdistanicum, x 4.4 (Sintenis 310)

9 P. asperum, x 4.4 (Lamond 1068)

10 P. heratense, x 4.4 (Kóie 3937)

11 P. crista-galli, x 4.4 (Hedge & Wendelbo W.4017)

12 P. latiflorum , x 4.4 (Kóie 2641)

13 P. himalayense, x 4.4 (Hedge & Wendelbo W.4541)

14 P. howardii, x 4.4 (Duthie 25 vii 1892)

15 P. cynoglossoides, x 4.4 (Lindberg 777/1960)

Figure 16,6

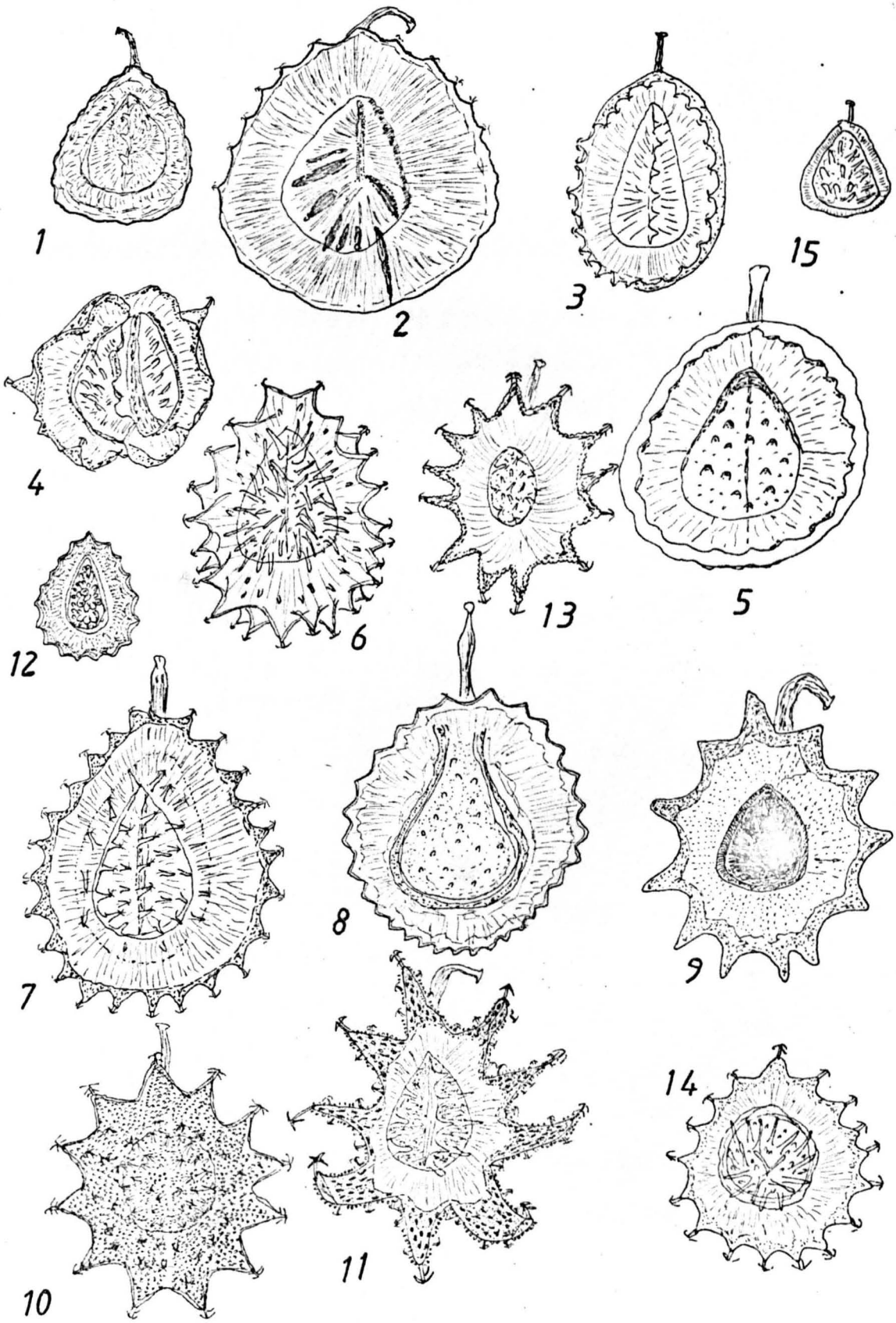


Figure 16.7

Paracaryum subgenera Modestomattiastrum and Paracaryum:

Nutlet Morphology

1 P. flaviflorum, x 4.4 (Rechinger 18446)

2 P. polyanthum, x 4.4 (5a) & x 17.5 (5b) (Rechinger 17688a)

3 P. rugulosum, x 4.4 (Manovsky et al.)

4 P. persicum, x 4.4 (Edmondson & Miller 1529)

5 P. platycalyx, group of nutlets x 4.4 (Lamond 883)

6 P. sintenisii, group of nutlets x 4.4 (Davis 28907) 6a margin of wing showing 3 rows of teeth, x 13

7 P. strictum, group of nutlets x 4.4 (Davis 21875)

8 P. hirsutum, dorsal and lateral views of nutlets x 4.4 (Davis 28623)

9 P. intermedium, groups of nutlets x 17.5: 9a heteromorphic 9b homomorphic (Lace 3699: Quetta)

10 P. stellatum, group of nutlets x 8.7 (Rechinger 33428)

11 P. papillosum, group of nutlets x 8.7 (Lace 3699: Hawai)

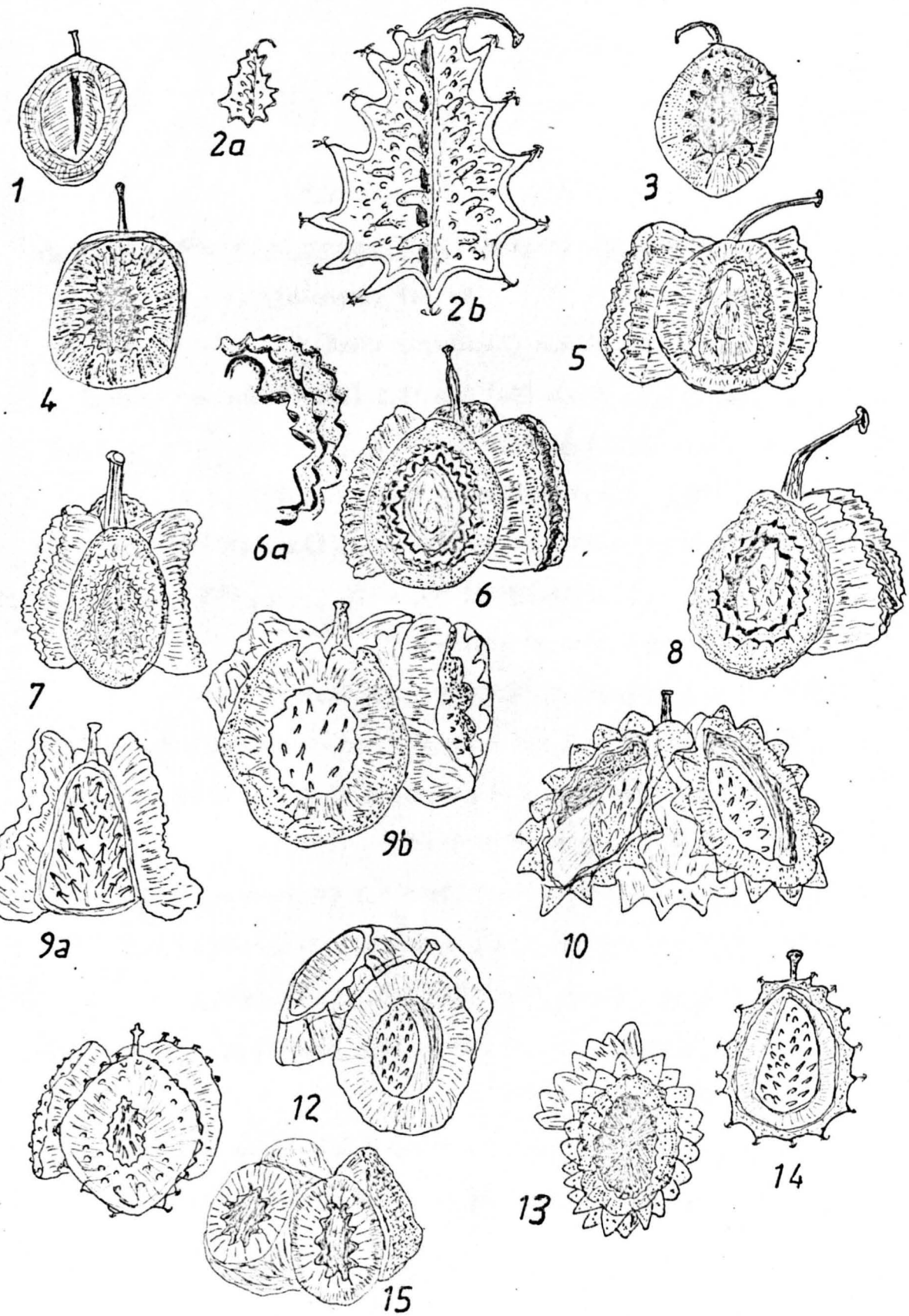
12 P. boissieri, group of nutlets x 8.7 (Davis 6794)

13 P. calathicarpum, dorsal and partial lateral views of nutlets, x 8.7 (Rechinger 36238)

14 P. bungei, dorsal view of nutlet, x 8.7 (Hedge & Wendelbo W.3177)

15 P. salsum, group of nutlets x 4.4 (Rechinger 5330b)

Figure 16,7



are used to separate many species of the latter sections (cf. RIEDL 1969). In P. stellatum (Fig. 16.7, no. 10) the wing bears triangular, horizontally patent gibbi which form a stellate false margin, while P. papillosum (Fig. 16.7, no. 11) is characterised by the wing being densely covered in minute papillae, rather than being bullate-rugose.

The disc (dorsal surface) of the nutlet is suborbicular in subgenus Mattiastrum, but ovate, lanceolate or trullate in the other subgenera. The surface may be glabrous (e.g. P. lamprocarpum: Fig. 16.6, no. 2, P. stenolophum: (Fig. 16.5, no. 9) but is usually sparsely to densely glochidiate. Glochids may be evenly scattered over the surface of the disc (P. artvinense, P. cappadocicum, P. cristatum, P. bungei (Fig. 16.7, no. 14), P. polyanthum (Fig. 16.7, no. 2), P. calycinum (Fig. 16.4, no. 3) etc.), or a central raised keel may be developed with the glochids largely or entirely confined to this (P. reuteri, P. polycarpum). This character, and the density of the glochids, have been used frequently to delimit species or subspecies, e.g. P. polycarpum (glochids confined to keel) and P. amani (glochids scattered); P. cristatum subsp. cristatum (glochids long, dense) and subsp. carduchorum (glochids short, sparse).

P. heratense (Fig. 16.6, no. 10) and P. multicaule (Fig. 16.5, no. 3) are the only two species to have the disc densely covered in "mealy" papillae interspersed with thin white glochidiate hairs. Although both belong to subgenus Modestomattiastrum, the two species do not seem to be closely related; P. heratense is allied to P. himalayense while P. multicaule is one of the Irano-Afghan caespitose species. This specialised indumentum has therefore almost certainly evolved independently in the two species.

P. sessiliflorum (Fig. 16.4, no. 9) and the species of subgen. Modestomattiastrum sect. Exalata, have very reduced nutlet wings. P. sessiliflorum is also unique in that the nutlets are enclosed by the linear erect calyx lobes when mature.

In all species the nutlets are attached to the gynobase by a well-developed ventro-apical scar and are coherent to the style as in Cynoglossum and Rindera. In most species all four nutlets normally mature and are all similar. Several species of sect. Microparacaryum, however, have heteromorphic nutlets. In these species, which include P. calathicarpum, P. serpentinicum and some forms of P. stellatum, two nutlets (distal) are winged, while in the other two (proximal) the wing is greatly reduced (Fig. 16.7, nos. 9, 9a); see also sect. 2.4.

16.5 PALYNOLOGY

16.5.1 Introduction:

The genus Paracaryum has received little palynological attention. AVETISIAN (1956) studied three species, P. himalayense, P. laxiflorum and P. rugulosum; his measurements are in close agreement with mine. BARBIER & MATHEZ (1973) studied 8 species of Mattiastrum and 4 of Paracaryum (s. str.) and referred all 12 to their pollen group B (pollen lacking in equatorial constriction). They observed, however, that Mattiastrum was heterogeneous with respect to the P/E ratio.

I have studied the pollen of 45 of the 69 species of Paracaryum as here defined; a summary of the quantitative data is given in Table 16.2. The genus is palynologically much more heterogeneous than was assumed from Barbier & Mathez's limited studies, which concentrated on subgenera Mattiastrum and Paracaryum. In particular, many species have been found to have dumb-bell shaped pollen classifiable in Barbier & Mathez's pollen group C.

Three major classes of pollen type occur in the genus:

1. elliptic pollen broadest at the equator, somewhat resembling that of Cynoglossum.
2. medium sized dumb-bell shaped grains, usually with a complete equatorial coller.
3. small dumb-bell shaped pollen with an incomplete equatorial collar.

Table 16.2

Quantitative Palynological Characters of Paracaryum

Species	C	P μm	E μm	B μm	D μm	P/E	P/B
incanum	-	16.9 (15.4-19.0)	13.6 (12.5-15.4)	-	13.7 (12.5-14.1)	1.24	-
corymbiforme	-	18.4 (17.5-20.0)	16.5 (15.0-18.1)	-	16.9 (15.9-17.5)	1.11	-
racemosum	-	15.7 (14.0-18.2)	13.6 (11.2-14.7)	-	13.8 (11.9-16.1)	1.15	-
longipes	-	13.3 (12.6-14.4)	11.9 (11.5-12.7)	-	12.6 (11.9-13.3)	1.12	-
calycinum	-	13.7 (12.0-15.4)	11.9 (10.5-13.4)	-	12.1 (10.5-14.0)	1.09-1.16	-
ancyritanum	-	12.4 (10.8-15.4)	11.2 (9.4-13.6)	-	11.3 (9.8-12.6)	1.09-1.33	-
paphlagonicum	-	12.1 (11.2-13.3)	10.8 (9.1-11.6)	-	10.8 (9.8-12.0)	1.08-1.27	-
aucheri	-	12.8 (11.5-13.4)	10.8 (10.4-11.2)	-	10.8 (10.2-11.2)	1.19	-
laxiflorum	-	13.3 (12.7-14.0)	10.6 (10.2-11.5)	-	11.6 (10.9-12.0)	1.25	-
sessiliflorum	-	13.2 (12.3-14.0)	10.9 (10.5-11.5)	-	9.1 (8.4-9.8)	1.21	-
dielsii	90	15.0 (14.0-15.8)	7.8 (7.0-8.3)	8.7 (8.4-9.1)	8.9 (8.8-9.0)	1.92	1.72
lithospermifolium	-	11.2 (9.1-12.9)	8.1 (6.4-11.3)	-	8.7 (7.0-10.8)	1.32	-
reuteri	-	11.1 (10.2-12.2)	8.4 (8.0-9.2)	-	9.7 (9.0-10.5)	1.31	-
polycarpum	-	10.1 (9.7-10.9)	7.6 (7.0-8.4)	-	7.8 (7.0-8.8)	1.33	-
cappadocicum	-	12.0 (11.6-12.6)	9.5 (8.7-10.3)	-	10.4 (9.1-11.9)	1.26	-
multicaule	-	8.8 (8.1-10.1)	7.0 (6.6-7.4)	-	7.0 (6.6-7.3)	1.26	-
nigrum	-	10.5 (10.2-10.9)	8.4 (7.7-8.7)	-	8.7 (8.1-9.1)	1.25	-
formosum	-	11.1 (10.4-12.2)	8.7 (7.6-9.0)	-	10.1 (9.7-10.5)	1.28	-

Table 16.2 (continued)

Species	C	P μm	E μm	B μm	D μm	P/E	P/B
turcomanicum	-	11.3 (10.9-11.5)	9.2 (8.7-9.5)	-	9.4 (9.1-9.7)	1.23	-
modestum	-	11.2 (9.5-12.3)	9.3 (8.1-10.2)	-	9.4 (8.4-10.5)	1.25	-
straussii	-	9.7 (9.1-10.5)	9.0 (8.4-9.5)	-	9.1 (8.8-9.8)	1.08	-
crista-galli	-	18.5 (17.5-19.9)	15.5 (14.7-16.8)	-	15.0 (13.6-16.8)	1.19	-
cristatum subsp. cristatum	95	12.6 (11.6-13.3)	6.7 (6.0-7.1)	7.3 (7.0-7.6)	7.6 (7.0-8.4)	1.87	1.77
-- subsp. carduchorum	-	10.6 (10.4-11.2)	6.9 (6.6-7.1)	-	8.7 (8.4-9.1)	1.44	-
kurdistanicum	97	11.5 (10.5-12.6)	6.9 (6.6-7.0)	7.1 (6.6-7.4)	6.9 (6.0-7.3)	1.67	1.62
asperum	85	11.6 (11.1-12.2)	5.9 (5.3-6.4)	6.9 (6.3-7.4)	7.0 (6.7-7.7)	1.97	1.74
heratense	90	9.7 (8.4-10.5)	5.3 (4.9-6.3)	5.9 (5.0-6.4)	5.5 (4.8-6.7)	1.83	1.64
latiflorum	83	11.7 (11.3-11.9)	5.9 (5.6-6.2)	7.1 (6.9-7.5)	7.1 (6.9-7.5)	1.98	1.65
howardii	89	11.6 (10.9-12.5)	5.5 (4.8-6.0)	6.2 (5.6-6.6)	6.7 (6.2-7.1)	2.11	1.87
himalayense	93	9.8 (8.7-11.2)	5.2 (4.2-5.5)	5.5 (4.8-6.3)	6.3 (5.7-6.7)	1.88	1.72
artvinense	91	9.2 (8.5-10.2)	5.2 (4.8-5.6)	5.7 (5.3-6.2)	6.7 (6.2-7.4)	1.77	1.61
subscaposum	88	13.0 (12.5-13.7)	6.4 (6.0-6.6)	7.3 (6.7-7.5)	7.4 (6.9-7.5)	2.03	1.78
flaviflorum	92	9.9 (9.7-10.8)	5.7 (5.6-6.0)	6.2 (5.9-6.7)	7.0 (6.9-7.3)	1.74	1.60
cynoglossoides	93	11.6 (11.3-11.9)	6.2 (5.9-6.6)	6.7 (6.2-7.5)	7.4 (6.9-7.5)	1.87	1.73
bungei	97	9.9 (9.1-10.8)	5.7 (4.9-7.0)	5.9 (5.2-6.3)	6.4 (5.9-7.0)	1.74	1.68
persicum	-	14.2 (13.6-14.8)	13.1 (12.3-14.0)	-	13.4 (12.3-14.7)	1.08	-
rugulosum	-	14.2 (12.6-16.8)	12.1 (10.2-13.3)	-	12.2 (11.2-13.3)	1.17	-

Table 16.2 (continued)

Species	C	P µm	E µm	B µm	D µm	P/E	P/B
platycalyx	88	11.8 (10.9-12.3)	5.9 (5.6-6.2)	6.7 (6.4-7.3)	7.1 (6.6-7.8)	2.00	1.76
sintenisii	89	12.1 (10.5-13.3)	6.3 (5.6-7.0)	7.0 (6.4-7.1)	7.0 (6.3-7.7)	1.91	1.76
hirsutum	97	12.7 (11.6-13.3)	6.6 (6.0-7.4)	6.8 (6.2-7.6)	7.4 (7.0-8.4)	1.92	1.90
strictum	90	11.2 (9.9-11.9)	6.1 (5.2-7.7)	6.7 (6.2-7.7)	7.0 (6.2-7.8)	1.67-2.07	1.53-1.75
salsum	93	11.9 (11.3-12.5)	6.6 (6.2-7.1)	7.1 (6.9-7.5)	7.6 (7.5-8.9)	1.80	1.68
serpentinicum	100	7.7 (7.1-8.7)	5.0 (4.3-5.7)	5.0 (4.3-5.7)	6.0 (5.3-6.3)	1.54	1.54
boissieri	98	8.0 (7.4-8.4)	5.0 (4.8-5.6)	5.1 (4.9-5.7)	4.9 (4.6-5.6)	1.60	1.57
calathicarpum	88	7.8 (7.3-8.4)	3.8 (3.4-4.2)	4.3 (4.2-4.6)	5.6 (4.6-6.3)	2.05	1.81
intermedium	90	7.7 (6.3-9.1)	5.0 (4.2-5.7)	5.0 (4.1-6.3)	4.9 (4.6-5.3)	1.54	1.38

Explanation of columns:

C = index of constriction

P = length of polar axis

E = equatorial breadth

B = maximum breadth

D = polar diameter

P/E = Erdtman's ratio

Sample size: 20 grains (10 equatorial view, 10 polar view) from each preparation. Several preparations were made for some species (see sect. 16.5.2 for details).

Within each group, particularly among the medium-sized dumb-bell shaped pollen, there is considerable specific variation. Within a given species, palynological variation is usually small and of a quantitative nature; a few species (e.g. P. strictum) show a broader range of variation and this may indicate that the limits of the species, as defined by gross morphology, need to be redefined. There is some overlap in quantitative characters between the pollen types described below; this reflects the close relationships between many of the pollen types and between the natural groups of specoes which they usually represent. The keys given here should therefore be treated more as informative than for practical identification. Unlike some genera, it is often difficult or even impossible to separate two species of Paracaryum palynologically.

16.5.2 Description:

Pollen small to rather large, elliptic, oblong or dumb-bell shaped, with or without equatorial constriction; heterocolpate, tricolporate, tripseudocolpate. Amb trigonal or hexagonal, straight or convex, acute or obtuse, often appearing peritreme, pseudocolpi included or excluded. P = 7-20 μm, E = 3.5-18 μm, B in constricted grains (3.5-)4.5-7(-8.5) μm, D = 4-18 μm. P/E = 1.05-2.11, P/B = 1.38-1.95 (pollen spheroidal, subprolate or prolate). Colpi rhombic, acute, diamond-shaped or narrowly linear. Endoapertures endocolpi or endopori, usually simple, rarely compound (P. crista-galli). Pseudocolpi narrowly rhombic to ± linear. Collar usually present and complete, or incomplete and vestigial, rarely absent altogether. NPC = 345. Sexine usually smooth.

1. Pollen elliptic, without equatorial constriction

2. Endoaperture compound ..... 3. 'crista-galli' type

2. Endoaperture simple

3. Amb hexagonal ..... 4. 'modestum' type

3. Amb trigonal

4. P = 11-20 µm; E = (9-)11-18 µm ..... 1. 'calycinum' type

4. P = 8-13 µm; E = 6.5-11 µm ..... 2. 'lithospermifolium' type

1. Pollen oblong, not broader at equator, usually equatorially constricted

5. P = 14-16 µm or more ..... 5. 'dielsii' type

5. P = 7-13(-14) µm

6. Pollen strongly constricted at equator (C = 85-80) ..... 8. 'asperum' type

6. Pollen not or weakly constricted at equator (C = 100-88)

7. Pollen 7-9 µm; equatorial collar incomplete or absent ..... 11. 'intermedium' type

7. Pollen 8-14 µm; equatorial collar usually complete

8. Endoaperture a distinctly lalongate endocolpus

9. Pollen 10.5-14 µm ..... 6. 'cristatum' type

9. Pollen 8-10.5(-11) µm ..... 9. 'flaviflorum' type

8. Endoaperture an endoporus or a small, only slightly lalongate endocolpus

10. Constriction weak to moderate (C = 93-88) ..... 7. 'himalayense' type

10. Constriction very weak (C = 100-97) ..... 10. 'bungei' type

1. 'calycinum' type (Subgenus Mattiastrum, P. persicum and P. rugulosum);

Species included and material examined:

P. corymbiforme DC. & A. DC. (Turkey, prov. Gümüşane: Köse Da., Sintenis 997!).

P. incanum Ledeb. (Turkey, prov. Ankara: Kavakli Dere, 31 v 1929, Bornmüller 14407!).

P. racemosum (Schreber) Britten (Turkey, prov. Yozgat: Akdağmadeni, Sofular De., vi 1960, E. & W. Curtis 167! 'Armenia', Calvert & Zohrab! prov. Amasya: Merzifon, Manissadjian 56! prov. Gümüşane: Bayburt Oluk Köprüsü, Tobey 2150!).

P. longipes Boiss. (Turkey, prov. Nevşehir, Sorger 64-32-36!).

P. calycinum Boiss. & Bal. (Turkey, prov. Samsun: Ladik, Ak Da., 1400 m, Tobey 1000! Vezirköprü at Kizil Irmak, 400 m, Tobey 2454! prov. Bolu: 34 km S. of Gerede, 1600 m, Sorger 62-82-1! prov. Ankara: Kizilcahamam, T. Baytop ISTE 13393! prov. Eskişehir: Eskişehir, 820 m, 14 v 1961, Kayacik !).

P. ancyritanum Boiss. (Turkey, prov. Çankiri: Ilgaz, T. Baytop ISTE 11293! Ilgaz to Çankiri, Davis 21474! prov. Ankara: Hacikadin De. nr Keciören, Davis 18828! 3 km N. of Nallihan, 900 m, Sorger 73-44-1! Ankara, Bornmüller 14412! prov. Amasya: Amasya, Görz 84!).

P. paphlagonicum (Bornm.) R. Mill (Turkey, prov. Çankiri: Ilgaz, 1000 m, 23 vi 1929, Bornmüller 14414! Ilgaz, 1000 m, Davis 21489! prov. Kastamonu: Tasköprü to Gökçeağaç, 600 m, Davis 38049! prov. Ankara: Çubuktell, Kotte 415!).

P. aucheri Boiss. (Aegean Islands: Samos, mt. Kerkis, 1220 m, Davis 1707!).

P. sessiliflorum (Rech. fil. & H. Riedl) R. Mill (Afghanistan, prov. Ghazni: W. of Sardalu pass between Qarabagh and Sang-i-Masha, 2600 m, 30 vi 1962, Rechinger 17385!).

P. laxiflorum Trautv. (Turkey, prov. Erzurum: Horasan to Pasinler, 1500-1700 m, Davis 30826!).

P. persicum Boiss. (Iran, Davis & Bokhari 56178!).

P. rugulosum (DC.) Boiss. (Turkey, prov. Ağri: 35 km E. of Doğubayazit nr Iran border, 1600 m, 31 v 1966, Davis 43981! Iran, Davis & Bokhari 56203!)

Pollen broadly elliptic, never with equatorial constriction. Amb trigonal, convex, obtuse, often appearing circular, pseudoapertures excluded. P = 10-20 μm, E = 9-18 μm, D = 8.5-17.5 μm. P/E = 1.08-1.33 (prolate-spheroidal to subprolate). Colpi rhombic, acute, diamond shaped, bordered by bacula and furrow. Endoaperture a $\pm$ lalongate, rhombic or elliptic endocolpus or a $\pm$ circular endoporus. Pseudocolpi $\pm$ narrowly rhombic,

diamond-shaped, often ± equalling colpi in breadth, bordered by bacula and furrow. Collar present.

1. Endoaperture a large rhombic endocolpus

2. Pollen prolate-spheroidal ..... persicum

2. Pollen subprolate ..... rugulosum

1. Endocolpus an elliptic endocolpus or an endoporus

3. Pollen 10.5-15.5 x 9-13.5 μm

4. Colpi broadly rhombic, short (½ x P), markedly different to long narrow pseudocolpi; edges of colpi nearly touching but not linked by collar ..... sessiliflorum

4. Colpi and pseudocolpi all rhombic, ± similar, ± equal in length, joined by equatorial collar ..... calycinum group

3. Pollen 14-20 μm x 11-18 μm

5. Endoaperture distinctly lalongate; pollen 14-18 x 11-15 μm ..... racemosum

5. Endoaperture nearly circular; pollen 15.5-20 x 12.5-18 μm

6. D = 12.5-14 μm ..... incanum

6. D = 16-17.5 μm ..... corymbiforme

The six species included in the P. calycinum group (P. ancyritanum, P. aucheri, P. calycinum, P. longipes, P. paphlagonicum and P. laxiflorum) all have very similar pollen and it is not possible to provide a workable key. In all species the pollen is 11-15 x 9-13 μm; that of P. calycinum, P. longipes and P. laxiflorum is larger than in the other three. P. longipes and P. aucheri have low values of P/E, tending to be prolate-spheroidal, while the pollen of P. laxiflorum is subprolate. In P. ancyritanum, P. calycinum and P. paphlagonicum the pollen varies from prolate-spheroidal to subprolate.

2. '*lithospermifolium*' type (Subgen. *Modestomattiastrum* p.p.)

Species included and material examined:

P. lithospermifolium (Lam.) Grande

---- subsp. *lithospermifolium* (Syria: W. of Ein Anbout above Bendan, 2740 m, 6 vi 1943, *Davis* 6141a!).

---- subsp. *cariense* (Boiss.) R. Mill (Turkey, prov. Kayseri: Bakir Da. nr. Akoluk Y., 30 vi 1952, *Davis, Dodds & Çetik, D.*19381! prov. Adana: Bakir Da. at top of Sencan De., 2100-2200 m, 30 vi 1952, *Davis* 19398! prov. Niğde: Ala Da., Narpiz gorge, 3050 m, 8 vi 1964, *Wood & Gibson* 188 & 191!).

P. reuteri Boiss. & Haussknecht. (Turkey, prov. Maraş: Berit Da., 1830-3050 m, 10 viii 1865, *Haussknecht*! ibid., nr Arpa Çukuru Y., 2300 m, 25 vii 1952, *Davis* 20282!).

P. polycarpum (Rech. fil.) R. Mill (Turkey, prov. Maraş: Akher Dagh (Ahir Da.), 1830 m, vii 1907, *Haradjian* 1602!).

P. cappadocicum Boiss. (Turkey, prov. Sivas: 42 km W. of Gürün, 1700 m *Sorger* 70-33-3!).

P. multicaule (Rech. fil.) R. Mill (Afghanistan: prov. Kandahar, hill to W. of town, S. of Argandheb bridge, 1200-1300 m, 20 iv 1969, *Hedge & Ekberg* W.7194!).

P. nigrum (H. Riedl) R. Mill (Afghanistan: Parvan, Panjshir valley, 3900 m, 22 vii 1965, *Hedge & Wendelbo* W.5430!).

P. formosum (Rech. fil. & H. Riedl) R. Mill (Afghanistan: Parvan, Salang pass, 80-110 km from Kabul, 3000 m, 25 vi 1965, *Lamond* 2101!).

P. turcomanicum Bornm. (USSR, Transcaspia: Aschabad, above Nephton, 4 v 1900, *Sintenis* 103!).

Pollen elliptic, without equatorial constriction. Amb trigonal, convex, obtuse. P = 8-13 μm, E = 6.5-11.5 μm, D = 6.5-12 μm. P/E = 1.23-1.33 (subprolate). Colpi rhombic, endoaperture a lalongate

endocolpus; pseudocolpi rhombic or narrowly rhombic. Collar present.

1. Sexine granular in appearance

2. D = 8-9 μm ..... nigrum

2. D = 9.5-10.5 μm ..... formosum

1. Sexine smooth or almost so

3. Pollen nearly prolate (P/E = 1.30 or higher)

..... lithospermifolium group (incl. reuteri, polycarpum)

3. Pollen distinctly subprolate (P = 1.23-1.26)

4. Pollen 8-10 x 6.5-7.5 μm ..... multicaule

4. Pollen 11-13 x 8.5-10.5 μm

5. P = 10.9-11.5 μm ..... turcomanicum

5. P = 11.5-13 μm ..... cappadocicum

The pollen of P. lithospermifolium, P. reuteri and P. polycarpum is practically indistinguishable.

3. 'crista-galli' type

Species included and material examined:

P. crista-galli (Rech. fil. & H. Riedl) R. Mill (Iran: M. Kuh-e Neyshabur, Darreh Abshar above Akhlamad, 1600-1800 m, Rechinger 4502!).

Pollen elliptic, not constricted at equator. Amb trigonal, convex, obtuse. P = 18.5 (17.5-19.9) μm, E = 15.5 (14.7-16.8) μm, D = 15.0 (13.6-16.8) μm. P/E = 1.19 (subprolate). Colpi broadly rhombic, bordered by bacula and furrows. Endoapertures compound, of two concentric lolongate endocolpi. Pseudocolpi very distinctly rhombic, very long, extending ± to poles, bordered to bacula and furrow. Collar present. Sexine smooth.

4. 'modestum' type (Subgen. Modestomattiastrum p.p.)

Species included and material examined:

P. modestum Boiss. & Hausskn. (Iran: in rupestribus Kaserun, iv 1868, Haussknecht! Luristan, Shah Bazan, Kőie 375! ibid., Morton 3770! 3793!).

P. straussii Hausskn. & Bornm. (Iran: Luristan, between Donud and Ayna, 9300 ft., Wright & Bent 530-305!).

Pollen elliptic, without equatorial constriction. Amb hexagonal (sometimes appearing triangular), convex, obtuse, pseudoapertures included. P = c. 9-12 μm, E = 8-10 μm, D = 8-10.5 μm. P/E = 1.08-1.25 (prolate-spheroidal to subprolate). Colpi rhombic, abruptly narrowed towards poles, bordered by bacula and furrow. Endoapertures a small lalongate endocolpus. Pseudoapertures very narrow, ±linear for most of their length, broadening at equator into a small diamond. Collar present. Sexine smooth.

1. Pollen prolate-spheroidal (P/E = c. 1.08) ..... straussii

1. Pollen subprolate (P/E = 1.20-1.33) ..... modestum

5. 'dielsii' type (Subgen. Mediomattiastrum)

Species included and material examined:

P. dielsii (Bornm.) R. Mill (Afghanistan: Deh Kundi, 50 km S.W. of Panjao, 3150 m, 30 vi 1967, Rechinger 36593!).

Pollen oblong, dumb-bell shaped, equatorial construction weak (C = c. 90). Amb hexagonal, appearing circular. P = 14-16 μm, E = 7-8.5 μm, B = 8.5-9 μm, D = c. 9 μm. P/E = 1.92, P/B = 1.72 (prolate). Colpi rhombic, bordered by bacula. Endoaperture an endoporus. Collar present. Sexine smooth.

6. 'cristatum' type (Subgenera Modestomattiastrum & Paracaryum p.p.)

Species included and material examined:

P. cristatum (Schreber) Boiss. (Turkey, prov. Erzurum: Palandöken Da., 25 km from Çat to Erzurum, 2350 m, Davis 47382! prov. Hakkari: Nehil Çayi, 48-55 km from Hakkari to Yüksekova, 1600-1700 m, 14 vi 1966, Davis 44889 - type of subsp. carduchorum R. Mill!).

P. kurdistanicum (Brand) R. Mill (Turkey, prov. Urfa: Siverek to Diyarbakir, N. slope of Karaca Da., 1250 m, Davis 28304!).

P. sintenisii Bornm. (Turkey, prov. Elaziğ: Elaziğ to Kale, 37 km from Elaziğ, 1150 m, 4 vi 1957, Davis & Hedge D.28907! Harput, Sintenis 1889: 295!).

P. hirsutum (DC.) Boiss. (Turkey, prov. Mardin: 8 km N.E. of Mardin, 1000 m, Davis 28623! prov. Siirt: above Sirnak, 1400-1500 m, Davis 42560!).

P. strictum (C. Koch) Boiss. (Turkey, prov. Çoruh: Artvin, 400 m, Stainton 8283! prov. Malatya: Gürün, 1067 m, Davis 21875! prov. Bitlis: Bitlis, 1500 m, Davis 44313! prov. Elaziğ: nr Harput, Aucher 2283!).

P. subscaposum (Rech. fil. & H.Riedl) R. Mill (Afghanistan: Orozgan, Kuh-Garm-ab, Lindberg 969!).

P. platycalyx Rech. fil. (W. Pakistan: Baluchistan, Quetta to Sibi, Belan pass, 1500 m, Lamond 713!).

Pollen oblong, dumb-bell shaped, equatorial constriction absent or weak (C = 100-88). Amb hexagonal, ± straight, acute. P = 10-13 µm, E = 5-7 µm, B = 6-8 µm, D = 6.5-9 µm. P/E = (1.55-)1.70-2.00, P/B = 1.53-1.90 (prolate). Colpi ± narrowly rhombic, diamond shaped to ± linear. Endoaperture a ± lalongate endocolpus. Collar present. Sexine smooth.

1. Equatorial constriction weak (C = 90-88)
  2. Pollen 12.5-14 x 6-6.5 µm; equatorial constriction apparently absent ..... subscaposum
  2. Pollen 10-13 x 5-7 µm..... platycalyx; sintenisii; strictum
1. Equatorial constriction absent or very weak (C = 100-95)
  3. P/E = c. 1.90 ..... hirsutum; cristatum subsp. cristatum
  3. P/E = 1.55-1.70
    4. P/E = c. 1.55 ..... cristatum subsp. carduchorum
    4. P/E = c. 1.62-1.70 ..... kurdistanicum

The pollen of P. hirsutum and P. cristatum is very similar; P. platycalyx, P. sintenisii and P. strictum also cannot be distinguished palynologically.

7. '*himalayense*' type (Subgen. *Modestomattiastrum*, p.p.)

Species included and material examined:

P. himalayense (Klotzsch & Garcke) C.B. Clarke (Afghanistan: Bamian, Bareki Cheidan on road to Band-e-Amir, 2800 m, 28 vi 1962, *Hedge & Wendelbo* W.4719! Nardak, Khash Kal bridge at Helmaud river, 2460 m, 6 vi 1969, *Hedge & Wendelbo* W.8661!).

P. heratense (Rech. fil. & H. Riedl) R. Kamelin (Afghanistan, Herat, 40 km S. of Herat, 1650 m, 14 v 1969, *Hedge & Wendelbo* W.7972!).

P. howardii (Kazmi) R. Mill (Pakistan: Gilgit Agency, distr. Astore, 2380 m, 25 vii 1892, *J.F. Duthie*!).

P. artvinense R. Mill (Turkey, prov. Çoruh: Ardanuç to Kordevan Da., 1100 m, 26 vi 1957, *Davis & Hedge* D.30085!).

P. salsum Boiss. (Iran: between Mayamey and Shahrud, *Rechinger* 5330b!).

Pollen oblong, dumb-bell shaped, equatorial constriction weak (C = 93-88). Amb hexagonal, convex, acute. P = 8-13 µm, E = 4-7 µm, B = c. 4.5-7.5 µm, D = c. 4.5-8 µm. P/E = 1.75-2.10, P/B = c. 1.60-1.90 (prolate). Colpi narrowly rhombic or ± linear. Endoaperture a small, slightly lalongate endocolpus or a ± circular endoporus. Pseudocolpi ± linear. Collar present. Sexine smooth.

1. Endoaperture a circular endoporus
   2. Colpi bordered by bacula ..... *himalayense*
   2. Colpi bordered by continuous muri ..... *heratense*
1. Endoaperture a slightly lalongate endocolpus
   3. P = 8.5-10.5 µm ..... *artvinense*
   3. P = 11-12.5 µm
      4. P/E greater than 2.00, E = 4.5-6 µm ..... *howardii*
      4. P/E less than 2.00, E = 6-7 µm ..... *salsum*

8. 'asperum' type

Species included and material examined:

P. asperum Stocks (Afghanistan, Kabul, Koh-i-Asamai, 1800 m, Hedge & Wendelbo W.4520!).

P. latiflorum (Rech. fil. & H. Riedl) R. Mill (Afghanistan, Ghazni, Kuh Mostoufi, Lindberg 260!).

Pollen oblong, dumb-bell shaped, equatorial constriction moderate (C = 85-83). Amb hexagonal, convex, acute. P = 11-12 μm, E = 5-6.5 μm, B = 6-7.5 μm, D = 6.5-7.7 μm. P/E = c. 1.95-2.00, P/B = 1.65-1.75 (prolate). Colpi linear. Endoaperture an endoporus. Pseudocolpi linear. Collar present.

The pollen of these two species is practically identical in morphology.

9. 'flaviflorum' type (Subgen. Modestomattiastrum sect. Exalata)

Species included and material examined:

P. flaviflorum (Rech. fil. & H. Riedl) R. Mill (Afghanistan, Bamian, Band-e-Amir, 2900 m, Hedge & Wendelbo W.4781!).

P. cynoglossoides (Rech. fil. & H. Riedl) R. Mill (Afghanistan, prov. Kandahar, Orozgan N.E. of Kandahar, Lindberg 1960: 777!).

Pollen oblong, dumb-bell shaped, equatorial constriction weak (C = 93-92). Amb hexagonal, convex, acute. P = c. 10-12 μm, E = c. 5.5-6.5 μm, B = c. 6-7.5 μm, D = c. 7-8 μm. P/E = c. 1.75-1.90, P/B = c. 1.60-1.75 (prolate). Colpi shortly rhombic, bordered by muri. Endoaperture a distinct lalongate endocolpus bordered by muri. Pseudocolpi similar to colpi. Collar present. Sexine smooth.

1. P = 9-11 μm ..... flaviflorum

1. P = 11-12 μm ..... cynoglossoides

10. 'bungei' type

Species included and material examined:

P. bungei Boiss. (Pakistan, Baluchistan, 10 km from Kalat to Surat, 2050 m, 22 iv 1965, Lamond 681!).

Pollen oblong, dumb-bell shaped, equatorial constriction very weak (C = 97). Amb hexagonal, convex, acute, ± circular. P = c. 9-11 μm, E = c. 5-7 μm, B = c. 5-7 μm, D = 6-7 μm. P/E = 1.74, P/B = 1.68 (prolate). Colpi narrowly rhombic. Endoaperture a small circular endoporus. Pseudocolpi ± linear. Collar apparently present and complete. Sexine punctate, granular in appearance.

11. 'intermedium' type (Subgen. Paracaryum sect. Microparacaryum).

Species included and material examined:

P. intermedium (Fresen.) Lipsky (Afghanistan: Pulalam, El, 2135 m, 15 vi 1937), Koelz 11853!).

P. boissieri Schweinfurth (Egypt: N. Galale, lower W. Nooz, 400-600 m, 27 iii 1944, Davis 6957!).

P. serpentinicum Rech. fil. (Afghanistan, prov. Kabul, 50 km from Kabul to Gardez, 1900 m, 28 vi 1965, Rechinger 31459!).

P. calathicarpum Stocks (Afghanistan: Panjao, 12 km E. of Panjao, 2650-2800 m, 21-22 vi 1967, Rechinger 36238!).

Pollen oblong, ± constricted at equator, equatorial constriction (when present) very weak or weak (C = 100-90). Amb hexagonal. P = 7-9 μm, E = 3.5-6 μm, B = 4-6.5 μm, D = 4.5-6.5 μm. P/E = 1.45-2.05, P/B = 1.38-1.81 (prolate). Colpi narrowly rhombic. Endoaperture a slightly lalongate endocolpus, rarely almost circular. Pseudocolpi linear. Collar incomplete, ± vestigial. Sexine smooth.

1. P/E = 2.00-2.10; E = 3.5-4.2 μm ..... calathicarpum

1. P/E = 1.50-1.60; E = 4-6 μm

2. Equatorial constriction weak but distinct (C = c. 90) ..... intermedium

2. Equatorial constriction absent or very weak (C = 100-98)

3. Endoaperture a nearly circular endoporus; D = 6.0(5.3-6.3) μm; equatorial constriction absent ..... serpentinicum

3. Endoaperture distinctly lalongate; D = 4.9(4.6-5.6) μ m;
equatorial constriction very weak ..... boissieri

16.5.3 Discussion:

In general, the eleven pollen types described above correspond with morphologically defined groups of species within the genus, although in some cases the pollen morphology cuts across the classification.

Pollen of the 'calycinum' type is largely confined to subgen. Mattiastrum and is the only pollen type found within that subgenus. Similar pollen also occurs in two closely related species of subgen. Paracaryum, i.e. P. persicum and P. rugulosum. P. persicum has been shown to provide a morphological link between these two subgenera and the similarity in pollen confirms this cross-relationship. Pollen of the 'calycinum' type is also found in P. sessiliflorum, which was included by RIEDL (1967) in Mattiastrum subgen. Mediomattiastrum along with M. dielsii Bornm. I have already discussed my reasons for excluding P. sessiliflorum from subgen. Mediomattiastrum (sect. 16.3). The occurrence of 'calycinum' type pollen supports my view that its true affinities lie in subgen. Mattiastrum, rather than with P. dielsii, which is the only species having oblong pollen of the 'dielsii' type.

By far the greatest variability in pollen morphology occurs in subgen. Modestomattiastrum. The 'lithospermifolium' type of pollen, which is very similar to that of Cynoglossum, is similar to the 'calycinum' type, differing principally in being smaller and more prolate. It can be considered a transitional stage from the 'calycinum' type to the 'cristatum' type; the 'modestum' type, in which the amb has become hexagonal, represents a further transitional stage along this evolutionary line. The pollen of many species of the 'lithospermifolium'type is very similar, reflecting the close morphological relationship between the species concerned.

Pollen morphology supports the view expressed in sect. 16.4.1 that

Riedl's subsect. Caespitosa should be dismembered. Some species of this subsection have 'lithospermifolium' type pollen (e.g. P. multicaule, P. formosum, P. nigrum) but P. subscaposum has equatorially constricted pollen which resembles the 'cristatum' type although it is larger than that of most species included in that group.

P. crista-galli is unique in the genus in having large elliptic pollen similar in size to P. incanum and P. corymbiforme (subgen. Mattiastrum) but with a compound endoaperture of two concentric lolongate endocolpi. This peculiar pollen confirms the isolated position of this species within subgen. Modestomattiastrum.

Pollen of the 'cristatum' type is found in several species of subgen. Modestomattiastrum, and in all examined species of subgen. Paracaryum sect. Paracaryum except P. persicum and P. rugulosum. Palynology therefore confirms the cross-relationship between P. cristatum, P. kurdistanicum etc. and subgen. Paracaryum, which has been established on the basis of gross morphology.

The 'asperum' pollen type is probably derived from the 'cristatum' type; it differs principally by the stronger constriction and the change from an endocolpus to an endoporus. It only occurs in two closely allied species which are themselves considered to be related to P. cristatum.

The 'himalayense' pollen type is characteristic of a group of related species within subgen. Modestomattiastrum having small pale blue corollas. This pollen type resembles the pollen of Paracynoglossum and is one of the most derived types in the genus Paracaryum. The 'flaviflorum' type, confined to sect. Exalata, represents another derivative of the 'cristatum' type.

Among the annual species a trend can be traced from P. salsum, which has pollen of the 'himalayense' type, through P. bungei to most species of sect. Microparacaryum, which have pollen of the 'intermedium' type.

The pollen becomes smaller - P. calathicarpum has the smallest pollen known in the genus - and there is gradual partial loss of the equatorial collar.

Pollen morphology seems to suggest that neither P. salsum nor P. bungei are closely allied to the species of sect. Microparacaryum.

16.6 CYTOLOGY

Previous cytological information purporting to refer to Paracaryum has all been based on P. coelestinum, which is here included in the genus Paracaryopsis. Until 1974 there were no published chromosome counts for the genus Paracaryum as delimited here. PODLECH & BADER (1974) and ARYAVAND (1977) have each studied three species (Table 16.3) and these remain the only published counts, so far as I am aware.

Table 16.3

Chromosome Numbers in the genus Paracaryum

Species	2n	Origin*	Provenance	Reference
asperum	24	W	Afghanistan: Kabul	Podlech & Bader 1974
flaviflorum	24	W	Afghanistan Bamian	Podlech & Bader 1974
rugulosum	24	W	Iran: Tehran	Aryavand 1977
sintenisii	24	W	Iran: nr Isfahan	Aryavand 1977
bungei	22	W	Iran: nr Isfahan	Aryavand 1977
intermedium	22	W	Afghanistan: Paktia	Podlech & Bader 1974

From these results it appears that Paracaryum is dibasic. The diploid number 2n = 24, the most common in the Cynoglosseae, has been recorded from four of the species. Dysploid reduction from 2n = 24 is the most probable explanation for the diploid number of 2n = 22 recorded from

* W = material of known wild origin

P. bungei and P. intermedium. The occurrence of the rather unusual number 2n = 22 in both P. bungei and P. intermedium suggests that subgen. Modestomattiastrum sect. Annua and subgen. Paracaryum sect. Microparacaryum are more nearly allied to each other than to the other sections of their respective subgenera.

16.7 RELATIONSHIPS

Relationships within the genus Paracaryum are complex and reticulate. The similarities and cross-relationships between taxa belonging to different subgenera or 'traditional genera' have been a considerable influence behind the treatment I have adopted here. Intrageneric and intergeneric relationships are discussed separately.

16.7.1 Intrageneric:

All four major taxa within the genus are linked by intermediate taxa possessing some characters of two or more of them. Subgenus Mattiastrum is linked to subgenus Modestomattiastrum by P. laxiflorum and P. montbretii. These species have the anthers and faucal scales of sect. Mattiastrum, but the flowers are the smallest in subgen. Mattiastrum and the style length is that typical of subgen. Modestomattiastrum.

The floral morphology of P. dielsii also links subgen. Mattiastrum with subgen. Modestomattiastrum. This species, which is sufficiently unique to justify the recognition of a monotypic subgenus (subgen. Mediomattiastrum), has the large long-tubed infundibular corollas and linear-oblong anthers of subgen. Mattiastrum, but the subquadrate scales and the anther attachment of subgen. Modestomattiastrum.

A different combination of floral characters, shared by P. persicum and P. cyclhymenium, connects subgen. Paracaryum with subgen. Mattiastrum. These two species have lingulate to trapeziform scales with the anthers borne above them (and often subexserted), condition only found in these

two species within subgen. Paracaryum but normal in subgen. Mattiastrum. The style, though relatively short, is exserted from the calyx, as in subgen. Mattiastrum, and the corollas are similar in size to the smaller-flowered species of that subgenus.

Many species-pairs, very similar in their habit and floral morphology, provide links between subgen. Modestomattiastrum and subgen. Paracaryum. Some examples of these species-pairs, which often cannot be separated except by their nutlets, include:

P. sintenisii (Subgen. Paracaryum) and P. asperum (Subgen. Modestomattiastrum)
P. hirsutum (" ") " P. cristatum (" ")
P. platycalyx (" ") " P. formosum (" ")
P. sect. Microparacaryum (" ") " P. bungei (" ")

P. bungei, which is a link between subgen. Modestomattiastrum and subgen. Paracaryum, is also somewhat related to P. cynoglossoides of sect. Exalata and to P. acrocladum, thus forming a transition between the biennial and annual species of subgen. Modestomattiastrum. P. artvinense is a similar intermediate between the 'himalayense' group, whose floral morphology it shares, and the perennials of the 'lithospermifolium' group, which it closely resembles in nutlet morphology.

Within subgenus Mattiastrum, four groups of related species can be identified:

1. P. incanum, P. corymbiforme and P. racemosum (large corollas, scales with appendages).
2. All other species of sect. Mattiastrum (smaller corollas, scales without appendages).
3. P. sessiliflorum (Sect. Sessiliflora).
4. P. laxiflorum and P. montbretii (Sect. Laxiflora).

RIEDL (1967) included P. sessiliflorum in Mattiastrum subgen. Mediomattiastrum along with Mattiastrum dielsii Bornm. (= P. dielsii (Bornm.) R. Mill).

The two species differ markedly in several characters as listed below (Table 16.4):

Table 16.4

Differential Characters of *Paracaryum dielsii* and *P. sessiliflorum*

Character	*P. dielsii*	*P. sessiliflorum*
Inflorescence	few-flowered, branched	many-flowered, unbranched
Pedicels at anthesis	2-3 mm	0
Calyx lobes	patent in fruit	erect in fruit, enclosing nutlet
Corolla colour	pale blue	dark violet
Corolla form	hypocrateriform	tubular
Corolla lobes	spreading	introflexed
Scales	subquadrate, exserted	oblong-linear, included
Anther position	below scale bases	above scale bases
Style length (in fl.)	8-9 mm	4-5.5 mm
Nutlets	longer than calyx, wing well developed	shorter than calyx, wing reduced
Pollen	dumb-bell shaped '*dielsii*' type	elliptic '*calycinum*' type

Several of these characters, notably those of anther insertion, scale morphology and pollen type, are common to subgen. *Mattiastrum* and the general affinities of *P. sessiliflorum* are apparently with that subgenus. However, because so many of its characters are unique in that subgenus (e.g. erect calyx lobes enclosing the nutlet; introflexed corolla lobes; nutlet with reduced wing), I have considered it worthy of sectional rank (as first suggested by RIEDL, 1967).

Several circles of allied species can be delimited within subgenus *Modestomattiastrum*, but, except for sect. *Exalata* and sect. *Annua*, there are so many cross-relationships and intermediates between groups that I have not given any of them formal recognition. The principal groups are:

1. '*lithospermifolium*' group (*P. lithospermifolium*, *P. shepardii*,

P. cappadocicum, P. amani, P. reuteri, P. stenolophum, P. polycarpum, P. lamprocarpum): a group of mostly very closely allied Turkish species, some of which on further collection may merit only subspecific or varietal rank.

2. 'cristatum' group (P. asperum, P. cristatum, P. kurdistanicum, P. latiflorum): a group of Turkish and Iranian species - P. cristatum/kurdistanicum and P. asperum/latiflorum form two species pairs. Connected to subgen. Paracaryum by P. cristatum.

3. 'multicaule' group (P. densum, P. formosum, P. karataviense, P. multicaule, P. nigrum): a group of caespitose species which are probably only distantly related to each other (except for P. karataviense and P. nigrum, which on further study may prove to be only variants of a single species). Loosely connected to the 'lithospermifolium' group, and to subgen. Paracaryum, by P. formosum.

4. 'himalayense' group (P. acrocladum, P. artvinense, P. heratense, P. himalayense, P. howardii) - a group of often much-branched biennials with small pale blue flowers. Connected to 'lithospermifolium' group by P. artvinense, and to 'cristatum' group by P. acrocladum.

Several species of subgen. Modestomattiastrum hold isolated taxonomic position. These include P. subsoaposum, with cylindrical corollas; P. crista-galli, which is unique in the genus in its pollen morphology; P. modestum and P. straussii, which are closely allied to each other but only distantly to the rest of the subgenus; and P. turcomanicum, very closely related to P. gracile but also somewhat intermediate between subgenus Mattiastrum and subgen. Modestomattiastrum.

Excluding the annual species, which form the very natural section Microparacaryum, two groups can be delimited in subgenus Paracaryum. Again, these have not been given formal recognition as they are connected by P. rugulosum:

1. 'persicum' group (P. cyclhymenium and P. persicum).

2. 'hirsutum' group (P. hirsutum, P. platycalyx, P. rugulosum, P. sintenisii, P. strictum, P. tenerum).

16.7.2 Intergeneric:

Paracaryum as defined here is a natural group fairly well separated from other genera of Cynoglosseae and recognisable by its facies. Floral characters, rather than those of the nutlets, are the best for delimiting it from Rindera. As POPOV (1953) observed, subgen. Mattiastrum is close to Rindera in its inflorescence and nutlets, but it sharply differs in the form and colour of the corolla. The corolla of Rindera normally has narrowly linear-lanceolate lobes, rather than the oblong to suborbicular lobes of Paracaryum, and the colour is usually lilac to yellowish, never violet or blue throughout as in P. subgen. Mattiastrum.

Paracaryum is readily distinguished from Cynoglossum and Paracynoglossum by its winged nutlets, but non-fruiting material of certain species is difficult to separate. The Cretan form of P. lithospermifolium is particularly difficult to distinguish from the sympatric endemic, Cynoglossum sphacioticum (GREUTER in MATHEZ 1976; Davis, pers. comm.). It is assumed that the extreme similarities are due to convergence in response to the same environmental stresses.

Certain species of Paracaryum, e.g. P. cynoglossoides, are transitional to genera in the Eritrichieae such as Lappula and Lepechiniella. They can be distinguished by their apical rather than median nutlet attachment.

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CORRIGENDUM

Chapter 17 - ADELOCARYUM

It has been drawn to my attention by Dr R.K. Brummitt (Royal Botanic Gardens, Kew) that, since Adelocaryum erythraeum Brand was not included in Brand's original protologue, and since all other species of the genus as conceived by Brand are excluded in the present thesis, the name Adelocaryum must be rejected and a new genus described. Therefore I here propose the name BRANDELLA R. Mill for Adelocaryum erythraeum.

BRANDELLA R. Mill, gen. nov. Syn: Adelocaryum Brand (excl. speciebus omnibus in descr. orig.) p.p. quoad A. erythraeum Brand.

Type: Brandella erythraea (Brand) R. Mill, comb. nov. Syn: Adelocaryum erythraeum Brand in Engler, Pflanzenreich 78 (IV. 252): 78 (1921). — Monotypic.

Herba biennis. Caulis erectus, ramosus, hirsutus. Folia (basalia tempo florifero emarcida) lanceolata-oblonga, setulis rigidulis sparsis e basibus calcaratis exorientibus. Inflorescentia cymorum terminalium axillarium scorpoidum; cymi in statu florif ro elongati recti laxi, ebracteati. Calyx ad basin in lobos breves ovato-oblongos fissus; lobi uninervati, setulosi. Corolla campanulata, p rvula, caerulea; limbus tubus aequans, ad basin in lobos ellipticos divisus. Fornices semilunares, parvae. Stamina in tubo corollae infra basin fornicium inserta. Gynobasis pyramidalis. Nuculae ad gynobasem cicatrice parva ventroapicale affixae, profunde p teriformes margine l to incrassato, disco semi-incluso; et discus et margo spinulis glochidiatis densis ferentes.

This amendment should be read in conjunction with sects. 17.1-17.2, portions of which it supersedes.

CHAPTER 17

9. ADELOCARYUM Brand emend. R. Mill

17.1 INTRODUCTION

The genus Adelocaryum is here considered to be monotypic; the single species, A. erythraeum is native to Ethiopia and adjacent Sudan (Map 22.1) and is a neglected taxon having a unique nutlet morphology which makes classification in any other genus difficult and unsatisfactory.

BRAND (1915) first proposed the genus for a diverse group of six species from C. Asia and India, namely Adelocaryum anchusoides (Lindl.) Brand, A. capusii (Franchet) Brand, A. schlagintweitii Brand, A. flexuosum Brand, A. coelestinum (Lindl.) Brand and A. malabaricum (C.B. Clarke) Brand. All these species are here considered to belong to other genera (Lindelofia, Paracynoglossum and Paracaryopsis). Later (BRAND 1921, p. 78) he described a seventh species, i.e. A. erythraeum Brand; it is this species which constitutes the genus Adelocaryum as recognised here.

Brand nowhere typified the genus. POPOV (1953) stated that A. anchusoides or A. coelestinum were possible choices and that if the former were chosen the generic name would have to be abolished since he had re-instated A. anchusoides as a member of Lindelofia; I agree that it does not warrant segregation at generic level. Popov believed that A. coelestinum could be recognised as a genus but he did not formally propose it as such, nor did he formally lectotypify Adelocaryum. In the present account A. coelestinum is treated as the type species of the new segregate genus Paracaryopsis (H. Riedl) R. Mill (sect. 18.2).

RIEDL (1962) briefly discussed the nomenclatural typification of Adelocaryum taking the logical but taxonomically unsound course of choosing the first species (A. anchusoides) in Brand's enumeration as provisional lectotype. In a later paper (RIEDL 1971) he merged all the species of Adelocaryum with Cynoglossum except for A. anchusoides which he classified

in Lindelofia. Two of these combinations were invalid as they had also been made a few months earlier by KAZMI (1971) but the validity of the combination Cynoglossum erythraeum (Brand) H. Riedl is not in dispute.

Riedl did not see material of A. erythraeum. His transfer of the species to Cynoglossum was based solely on Brand's diagnosis in the Pflanzenreich (1921). Examination of material preserved at Kew clearly shows that this taxon cannot be classified in Cynoglossum. It has nutlets which, instead of being both wingless and ± densely glochidiate as in Cynoglossum, have a broad thickened incurved margin as in Omphalodes and Paracaryum. However, unlike any other species of Cynoglosseae known to me, the wing and disc are both covered in fairly dense spiny glochids. The presence of a wing precludes classification in Cynoglossum or any of its allies, and since classification in Paracaryum is also made difficult by the presence of the spines on the wing I retain the name Adelocaryum for this species, which by exclusion of all other species from the genus becomes a neotype.

Excluded species:

A. anchusoides (Lindl.) Brand in Feddes Rep. 13: 548 (1915) = Lindelofia anchusoides (Lindl.) Lehm.

A. capusii (Franchet) Brand, loc. cit. (1915) = Lindelofia tschimganica M. Popov ex Pazij

A. coelestinum (Lindl.) Brand, loc. cit. (1915) = Paracaryopsis coelestina (Lindl.) R. Mill (sect. 18.2)

A. flexuosum Brand in Feddes Rep. 14: 149 (1915) = Paracynoglossum flexuosum (Brand) R. Mill (sect. 20.2)

A. malabaricum (C.B. Clarke) Brand in Feddes Rep. 13: 549 (1915) = Paracaryopsis malabarica (C.B. Clarke) R. Mill (sect. 18.2)

A. schlagintweitii Brand, op. cit. 548 (1915) = Paracynoglossum schlagintweitii (Brand) R. Mill (sect. 20.2).

17.2 SYSTEMATIC TREATMENT

Adelocaryum Brand emend. R. Mill, excl. speciebus in descriptione originale (Feddes Rep. 13: 547-549, 1915). Syn: Adelocaryum Brand in Engler, Pflanzenreich 78 (IV. 252): 76-79 (1921) p.p. quoad A. erythraeum Brand.

Neotype designated here: A. erythraeum Brand in Engler, Pflanzenreich 78 (IV. 252): 78 (1921). Monotypic.

Biennial herb. Stem erect, branched, hirsute. Leaves (basal withered at flowering time) lanceolate-oblong, with sparse rigid setules arising from calcareous bases. Inflorescence of terminal and axillary scorpioid cymes which straighten and elongate, becoming lax in fruit, ebracteate. Calyx divided to base into short (2-3 mm) ovate-oblong lobes; lobes 1-veined, setulose, ciliate. Corolla campanulate, rather small (3-4 mm), blue; limb equalling tube, divided to base into elliptic lobes. Faucal scales small, semilunar. Stamens inserted in corolla tube below bases of scales. Style ½ x calyx, stigma capitate. Gynobase pyramidal. Nutlets 4, attached to gynobase by small ventro-apical attachment scar, deeply pateriform with broad thickened margin (analogous to that of Omphalodes and Paracaryum subgen. Paracaryum) which partly encloses disc; disc and margin both densely covered with short spinules bearing glochids.

17.3 MORPHOLOGY AND RELATIONSHIPS

In habit, Adelocaryum closely resembles Paracaryum, but is readily distinguished by the nutlets which bear glochid-tipped spinules on both disc and margin, a combination apparently unique in any species of Cynoglosseae having callous-margined nutlets (Fig. 18.1, nos. 4 & 5).

The leaves and corolla morphology indicate possible relationships with Paracaryum or Paracynoglossum. The leaf setules arise from multicellular tuberculate bases similar to those found in the latter genera. The leaves are not triplinerved (as in many species of Paracynoglossum), however,

The blue corollas also resemble those of many species of Paracynoglossum, and the semilunar faucal scales are similar to those found in some of the African species of that genus, e.g. P. lanceolatum.

There seems to be little or no affinity with any of the other six species which Brand included in his concept of Adelocaryum. Brand himself was aware of the heterogeneity of nutlet types in his new genus and indeed, the generic name reflects this. The species under consideration here cannot satisfactorily be accommodated in any of the three genera (Lindelofia, Paracaryopsis and Paracynoglossum) to which Brand's other six species of Adelocaryum have been variously transferred, as all are characterised by nutlets lacking a callous margin. Adelocaryum erythraeum is distinct from species of genera possessing such a margin (Desmolopha, Omphalodes and Paracaryum) on account of the dense marginal glochidiate spinules. In view of this, and considering its geographic isolation from the other callous-margined genera, it seems best to award it generic recognition.

CHAPTER 18

10. PARACARYOPSIS (H. Riedl) R. Mill

18.1 INTRODUCTION

The genus Paracaryopsis is endemic to the west coast of India from Bombay S. to Kerala (Malabar) (Map 18.1) and comprises three species - P. coelestina, P. lambertiana and P. malabarica - which were previously classified in Adelocaryum Brand, Cynoglossum L. or Paracaryum (DC.) Boiss.

The three species were all initially classified in Paracaryum by CLARKE (1883), although he remarked that the genus of P. lambertianum was doubtful. This treatment was followed by COOKE (1905), who provides the most detailed account of the three species.

BRAND (1921) transferred Paracaryum lambertianum to Mattiastrum Brand and referred P. coelestinum and P. malabaricum to Adelocaryum Brand. RIEDL (1962) transferred P. coelestinum from Adelocaryum to Cynoglossum subgen. Eleutherostylum, where it was placed in a monotypic section, sect. Paracaryopsis H. Riedl. In his discussion of Adelocaryum (RIEDL, 1971) he also removed Paracaryum malabaricum to Cynoglossum, and stated that it was very similar to, and clearly related to, C. coelestinum. Thus, although it was not actually stated, he implied that it should be classified in sect. Paracaryopsis.

Clarke's third species, P. lambertianum, seems to have been taxonomically neglected since Brand removed it to Mattiastrum. I have examined several collections of this species and agree with Clarke and Cooke that it is related to the other two species which they had included in Paracaryum. The latter, although sharing the character of somewhat winged nutlets, differ from Paracaryum in that the nutlets, while appearing coherent to the style, do not separate by an awn at maturity. Although differing by its larger, smooth, awned nutlets, Mattiastrum lambertianum (C.B. Clarke) Brand is undoubtedly very closely allied to the other two species in habit

and corolla morphology, and should be classified in the same taxon. All three species are very different to any species of Paracaryum as here delimited and should be excluded from that genus. The development of winged nutlets has presumably taken place independently.

Riedl's subgen. Eleutherostylum of Cynoglossum has been shown to be a heterogeneous assemblage (see sects. 13.1, 2.4, 2.5.1b, 15.1). The species treated here have nothing in common with the genus Eleutherostylum as here delimited, but rather share several vegetative characters with Paracynoglossum. As they differ from that genus in several floral and fruit characters, as well as possessing a characteristic type of pollen, I have considered Riedl's section Paracaryopsis worthy of generic rank.

Accepted taxa:

P. coelestina (Lindl.) R. Mill

P. lambertiana (C.B. Clarke) R. Mill

P. malabarica (C.B. Clarke) R. Mill

18.2 SYSTEMATIC TREATMENT

Paracaryopsis (H. Riedl) R. Mill, gen. nov. Syn: Cynoglossum L. subgen. Eleutherostylum (Brand) H. Riedl sect. Paracaryopsis H. Riedl in Öst. Bot. Zeitschr. 102: 393 (1962).

Type: P. coelestina (Lindl.) R. Mill.

Tall perennial herbs (sometimes biennial?). Rootstock stout, clothed with leaf bases. Stems stout, erect, ± branched, 30-150 cm, glabrous (especially below and on old stems) or strigose, adpressed-pubescent in inflorescence. Radical leaves large, long-petiolate; petioles 6-30 cm, lamina 10-40 x 5-20 cm, lanceolate, broadly ovate or triangular, acute or acuminate, cordate or cuneate; upper surface shortly but ± densely adpressed strigose or setulose, hairs arising from white calcifying tuberculate bases; lower surface with numerous prominently raised camptodromous veins, subglabrous on surface but densely hairy on veins, hairs arising from

tuberculate bases. Cauline leaves sessile or lower shortly petiolate, similar in shape and indumentum to basal leaves but smaller and decreasing in size towards inflorescence. Flowers in ebracteate, hairy, often two-forked scorpioid cymes which sometimes form a dense corymb. Pedicels adpressed-strigose, short, sometimes nodding (P. lambertiana). Calyx divided to c. $\frac{3}{4}$, slightly accrescent (up to 2 x) in fruit, lobes ovate or ovate-oblong, obtuse or subacute, densely hairy. Corolla pale or dark blue, 4-12 mm long, campanulate or subrotate, tube subequal to limb. Faucal appendages (scales) subquadrate with emarginate apex. Stamens wholly included or with their anthers scarcely exserted, filaments very short, inserted in middle of tube; anthers oblong-ovoid, without basal or apical appendages. Gynobase pyramidal. Ovules 4, but 2 nutlets sometimes aborting (especially in P. lambertiana). Nutlets apparently coherent to gynobase but separating easily, with or without an awn; attachment scar ± large and elevated, ventro-apical; nutlets ovoid, broadly ovate or suborbicular, 5-12 mm diam., napiform or scaphiform or flat, with a prominent erect or flat marginal wing, margin often incurving over disc, glochidiate or smooth; disc glochidiate or smooth.

1. Nutlets 10-12 mm diam., smooth, with ± flat margin, separating from style by an awn; radical leaves cuneate at base ..... 3. lambertiana

1. Nutlets 5-6 mm diam., glochidiate, with erect, ± incurving margin, not separating from style by an awn; radical leaves deeply cordate at base

2. Flowers 4-5 mm long, pale blue with darker centre; stems 100-150 cm, reddish ..... 1. coelestina

2. Flowers 9-11 mm long, uniformly dark blue; stems 30-100 cm, usually greenish ..... 2. malabarica

1. P. coelestina (Lindl.) R. Mill, comb. nov. Syn: Cynoglossum coelestinum Lindl., Bot. Reg. 25: t. 36 (1839); Echinospermum coelestinum (Lindl.) Wight, Icon. 4: t. 1394 (1850); Paracaryum coelestinum (Lindl.) Bentham & Hooker fil., Gen. Pl. 2: 850 (1876) in adnot.; C.B. Clarke in Hooker fil., Fl. Brit. Ind. 4: 160 (1883); Adelocaryum coelestinum (Lindl.) Brand in Feddes Rep. 13: 549 (1915).
2. P. malabarica (C.B. Clarke) R. Mill, comb. nov. Syn: Paracaryum malabaricum C.B. Clarke in Hooker fil., Fl. Brit. India 4: 160 (1883); Adelocaryum malabaricum (C.B. Clarke) Brand in Feddes Rep. 13: 549 (1915); Cynoglossum malabaricum (C.B. Clarke) H. Riedl in Öst. Bot. Zeitschr. 119: 71 (1971).
3. P. lambertiana (C.B. Clarke) R. Mill, comb. nov. Syn: Paracaryum lambertianum C.B. Clarke, op. cit. 161 (1883); Mattiastrum lambertianum (C.B. Clarke) Brand in Engler, Pflanzenreich 78: (IV. 252): 61 (1921).

18.3 MORPHOLOGY

The three species of Paracaryopsis share a distinctive facies which is reminiscent of some species of Paracynoglossum.

18.3.1 Rootstock:

The roots have rarely been collected but the rootstock appears to be stout and perennial in all species (some accounts state 'doubtfully biennial'), and is clothed with old leaf bases in a similar manner to the perennial species of Cynoglossum and Paracynoglossum.

18.3.2 Stems:

Each rootstock apparently produces one or few stems. These are stout and tall, reaching 1 m (1.5 m in P. coelestina), and apart from being often glabrescent are similar to those of Paracynoglossum sect. Latifolia.

18.3.3 Leaves:

The cordate radical leaves of P. coelestina and P. malabarica are very distinctive, and somewhat resemble those of Paracynoglossum

sect. Latifolia. The oblong, cuneate leaves of P. malabarica more resemble P. sect. Paracynoglossum. All have a very characteristic venation pattern, similar to that of many species of Paracynoglossum sect. Paracynoglossum but differing by the greater number of veins. The reticulate side-veins are also elevated and pilose, contrasting with the subglabrous lower surface of the lamina. These distinct elevated veins separate Paracaryopsis from sect. Latifolia of Paracynoglossum while most species of sect. Paracynoglossum differ in having only 3 principal longitudinal veins. The tuberculate trichomes resemble those of Paracynoglossum.

18.3.4 Inflorescence:

In all species the inflorescence is composed of terminal and lateral scorpioid cymes, relatively few in P. coelestina and P. lambertiana , but numerous and forming a paniculate pseudocorymb in P. malabarica. The cymes are ebracteate, as in most species of Paracynoglossum.

18.3.5 Calyx:

The calyx is divided to c. $\frac{3}{4}$, i.e. not quite so deeply as in most species of Paracynoglossum. The lobes usually have numerous veins (reduced to 3 in P. malabarica), whereas in Paracynoglossum the calyx lobes have only a single vein (often apparently absent) or rarely 3 (as in P. rochelia).

18.3.6 Corolla:

In all three species the corolla is brachymorphic and campanulate, although subrotate in P. lambertiana. In P. lambertiana and P. coelestina it is pale blue with a darker centre, while in P. malabarica it is a uniform dark blue. P. coelestina has the smallest corollas (4-6 mm), while in the other two species they are 9-11 mm long, much larger than in any species of Paracynoglossum except for some species of sect. Latifolia. The scales are subquadrate and emarginate, resembling those of Paracynoglossum, and the anthers are included or barely exserted, the latter condition only occurring in P. malabarica.

Figure 18.1

Paracaryopsis, Adelocaryum, Ivanjohnstonia and Suchtelenia:

Nutlet Morphology

1 Paracaryopsis coelestina: dorsal view of nutlet, x 8.7 (Sedgwick & Bell 4506)

2 Paracaryopsis malabarica: dorsal view of nutlet, x 8.7 (Law s.n.)

3 Paracaryopsis lambertiana: dorsal view of nutlet, x 4.4 (College of Science, Poona)

4 Adelocaryum erythraeum: group of nutlets in dorsal and dorso-lateral views, x 8.7 (Andrews 3490)

5 Adelocaryum erythraeum: ventral surface of nutlet, x 8.7 (Andrews 3490)

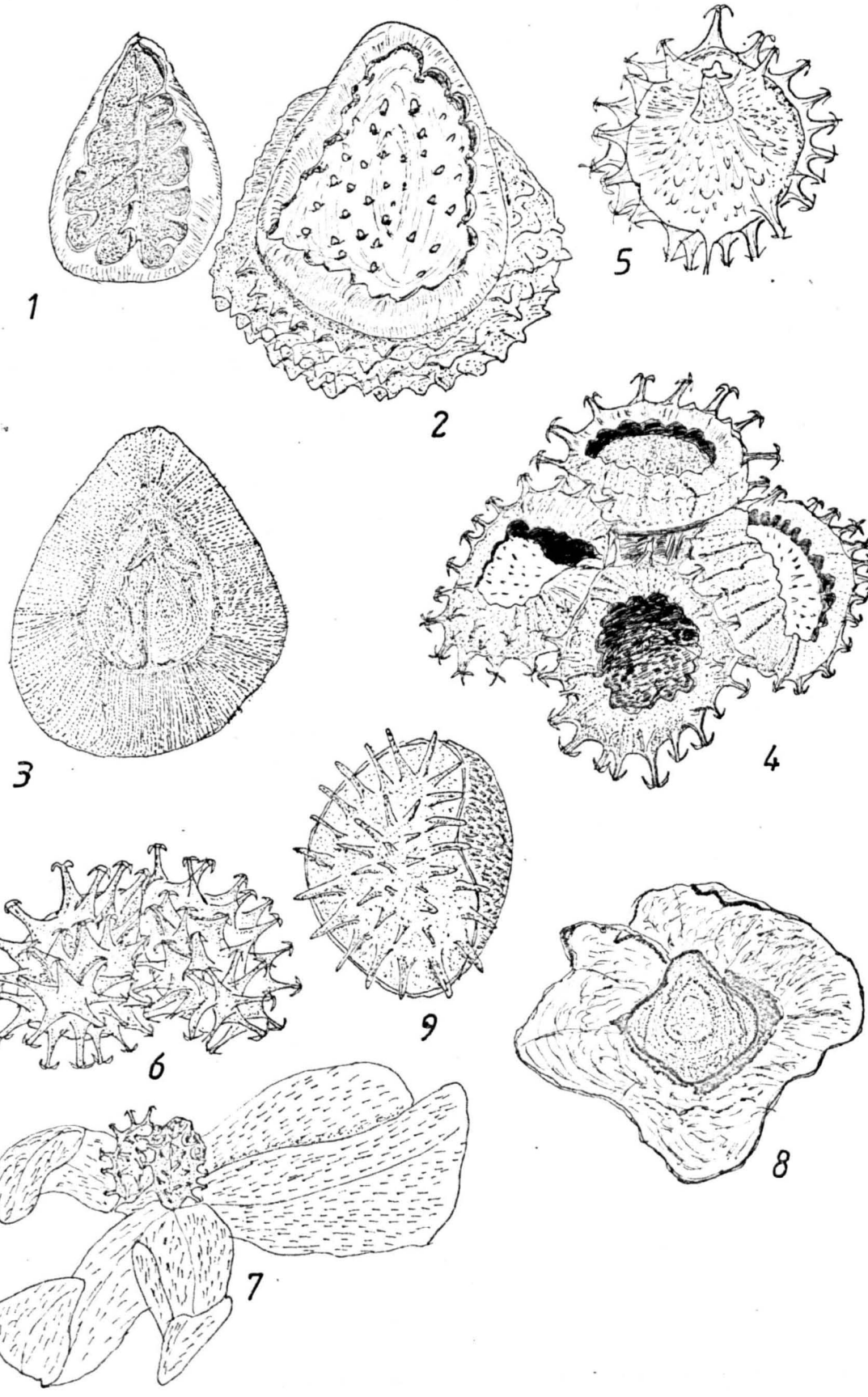
6 Ivanjohnstonia jaunsariensis: group of nutlets, x 17.5 (Gamble 27383)

7 Ivanjohnstonia jaunsariensis: nutlets and accrescent calyx, x 4.4 (Gamble 27383)

8 Suchtelenia calycina: var. calycina: nutlet and accrescent calyx, x 4.4 (Polyanev 673)

9 Suchtelenia calycina var. acanthocarpa: dorsal and part-lateral surfaces, x 8.7 (Sintenis 1901: 600)

Figure 18,1



18.3.7 Nutlets:

The nutlets are the most distinctive feature of Paracaryopsis. In all three species the margin is developed into a wing, as in Paracaryum, a situation not found in any species of Cynoglossum or Paracynoglossum. In P. coelestina (Fig. 18.1, no. 1) and P. malabarica (Fig. 18.1, no. 2) the wing is erect and ± incurving over the disc, analogous to Paracaryum subgen. Paracaryum. The degree of incurving is not as great as in Paracaryum, however. Glochids are present on the incurved edge of the margin.

P. lambertiana (Fig. 18.1, no. 3) is very different in its nutlet morphology and this has led to doubt as to its taxonomic position. COOKE (1905) noted that, in material cultivated at Mahableshwar, India, only two nutlets normally matured, the other two usually being suppressed. The two visible nutlets are much larger than in the other two species (up to 12 mm diam.), flattened, with a completely smooth disc and broad glabrous flat wing. The latter influenced BRAND (1921) when he transferred the species to Mattiastrum. Furthermore, the species differs from the other two by the presence of an awn at the apex of the attachment scar.

The difference in nutlet morphology between P. Lambertiana and the other two species is similar to that which distinguishes Madrea from Omphalodes and Paracaryum subgenus Paracaryum from subgen. Mattiastrum. In view of the small size of the genus and the similarities in floral and vegetative morphology between the taxa concerned, I do not consider that any infrageneric taxa are justified.

18.4 PALYNOLOGY

BARBIER & MATHEZ (1973) studied the pollen of P. coelestina but did not publish detailed results. They referred the pollen to their pollen type C (dumb-bell shaped). The other two taxa do not appear to have been examined previously. I have studied the pollen of all three species; the

quantitative data are summarised in Table 18.1.

Material examined:

P. coelestina (Lindl.) R. Mill (Vesey-Fitzgerald 24[18]/4!).

P. malabarica (C.B. Clarke) R. Mill (unlocalised, College of Science, Poona!).

P. lambertiana (C.B. Clarke) R. Mill (unlocalised, College of Science, Poona!)

18.4.1 Description:

Pollen oblong, dumb-bell shaped, equatorial constriction weak to strong (C = 95-79); heterocolpate, tricolporate, tripseudocolpate, pseudoapertures included. Amb hexagonal, straight or convex, acute or obtuse, P = 7-10 μm, E = 3-4.5 μm, B = 3.5-5.5 μm, D = 4-6 μm. P/E = c. 2.05-2.45, P/B = c. 1.70-2.30 (prolate or perprolate). Colpi very narrowly rhombic to linear, sometimes indistinct, bordered by furrow or by indistinct ridge. Endoaperture an endocolpus or an endoporus, sometimes very indistinct. Pseudocolpi linear. Collar absent. Sexine smooth. NPC = 345.

1. Pollen perprolate (P/B = c. 2.30) ..... lambertiana

1. Pollen prolate (P/B = c. 1.70-1.80)

2. P/E = c. 2.10, P/B = c. 1.70 ..... coelestina

2. P/E = c. 2.25, P/B = c. 1.80 ..... malabarica

Table 18.1

Quantitative Palynological Characters of Paracaryopsis

Species	C	P μm	E μm	B μm	D μm	P/E	P/B
coelestina	81	8.1(7.4-8.8)	3.9(3.6-4.5)	4.8(4.4-5.4)	5.8(5.6-6.0)	2.08	1.68
malabarica	79	8.5(7.8-9.0)	3.8(3.4-4.3)	4.8(4.5-5.0)	5.0(4.2-5.0)	2.24	1.77
lambertiana	95	8.7(8.3-9.8)	3.6(3.4-4.2)	3.8(3.4-4.2)	4.3(4.2-4.5)	2.42	2.29

C = index of constriction

P = length of polar axis

B = maximum breadth

P/E = Erdtman's ratio

E = equatorial breadth

D = polar diameter

18.4.2 Discussion:

The pollen of P. coelestina closely resembles many species of Paracynoglossum in being dumb-bell shaped and relatively small, with linear colpi bordered by furrow only, and lacking an equatorial collar. The equatorial constriction is considerably stronger than in most members of Paracynoglossum, exceptions being P. borbonicum (sect. Paracynoglossum) and P. nervosum and P. stewartii of sect. Latifolia. The pollen is quite different from the larger, ± oblong grains of Eleutherostylum as here defined and supports the relationship with Paracynoglossum suggested by the vegetative morphology.

The pollen of P. malabarica resembles that of P. coelestina in being strongly equatorially constricted with a straight-edged amb. The P/E ratio is higher, however, and the polar diameter, D, is noticeably smaller. The most distinctive feature is the slender, apparently continuous ridges (rather than a furrow) bordering the linear colpi. These may have developed from the individual bacula which commonly border the colpi of Cynoglossum and some Paracynoglossum. Alternatively, they may represent bacula so small and close together that they are beyond the resolving power of the light microscope. The Cynoglosseae do not as a whole yield good material for the scanning electron microscope and I was not able to prepare satisfactory material of P. malabarica. The ridges are also a feature of P. lambertiana.

Palynology confirms the relationship of P. lambertiana with the other species of Paracaryopsis. Both P. lambertiana and P. malabarica have continuous slender ridges bordering the colpi, and are the only two species in the Cynoglossum circle of genera to possess this character, although similar ridges occur in Omphalodes. They have not been observed in any species of Paracaryum and this supports their exclusion from that genus.

The pollen of P. lambertiana is similar in size to that of P. malabarica,

but differs by its weaker equatorial constriction and its much higher values of P/E and P/B (both higher than in any species of Paracynoglossum). Its pollen can be considered the most highly advanced in the genus; that of P. coelestina is apparently the least derived, being larger with slightly rhombic colpi, but it is perhaps more advanced than P. lambertiana in its degree of constriction. P. malabarica is intermediate, having the small size of P. lambertiana but a relatively low P/E value similar to but slightly higher than that of P. coelestina.

18.5 CYTOLOGY

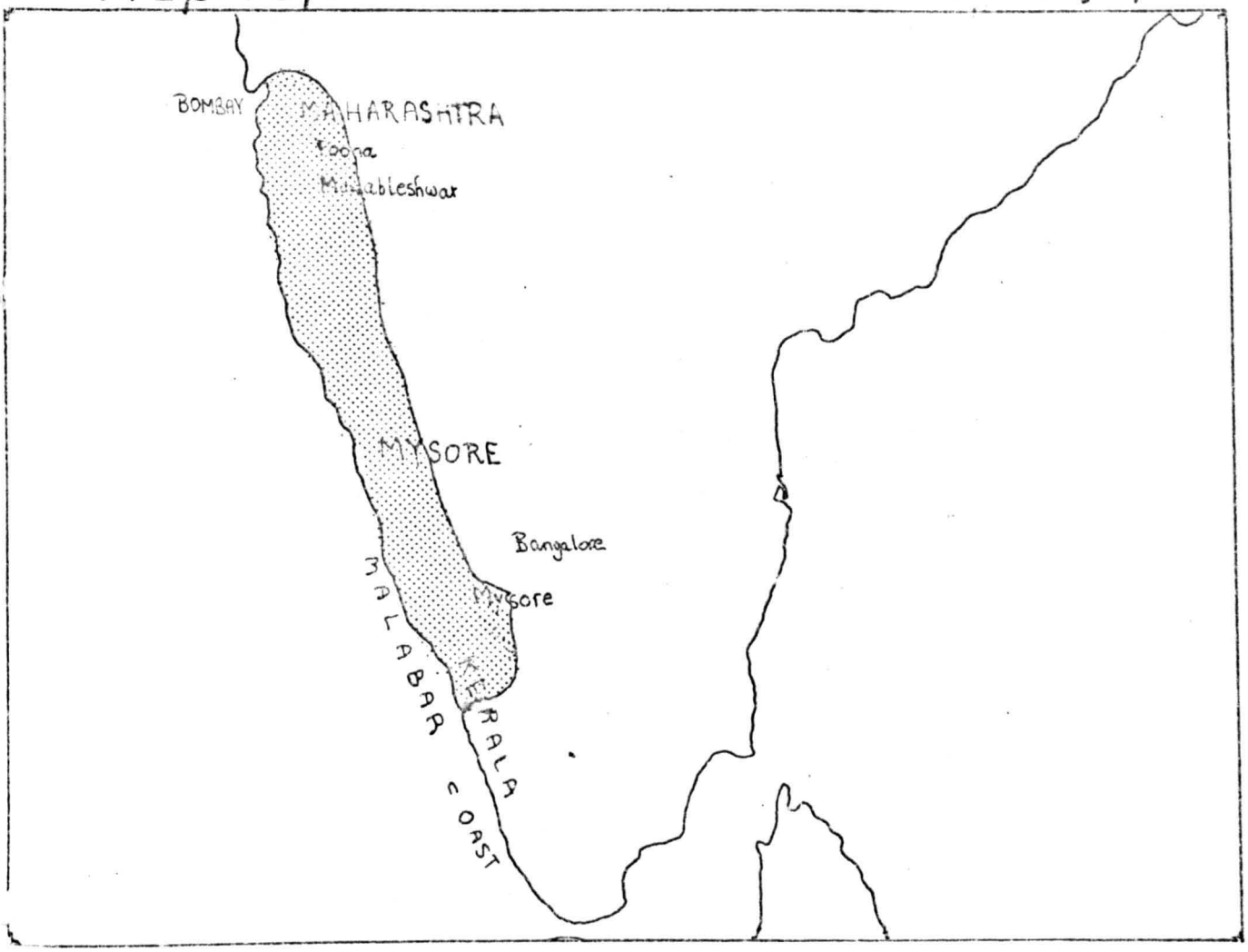
Of the three species of Paracaryopsis, only P. coelestina has been studied cytologically. Both STREY (1931) and ZHUKOVA (1967) record a diploid number of $2n = 24$ from material cultivated in Germany and at the Arctic-Alpine Botanical Garden (Leningrad), respectively. Paracaryopsis is therefore diploid with the same chromosome number as most of the Cynoglosseae. The chromosomes are small - and advanced character.

18.6 RELATIONSHIPS

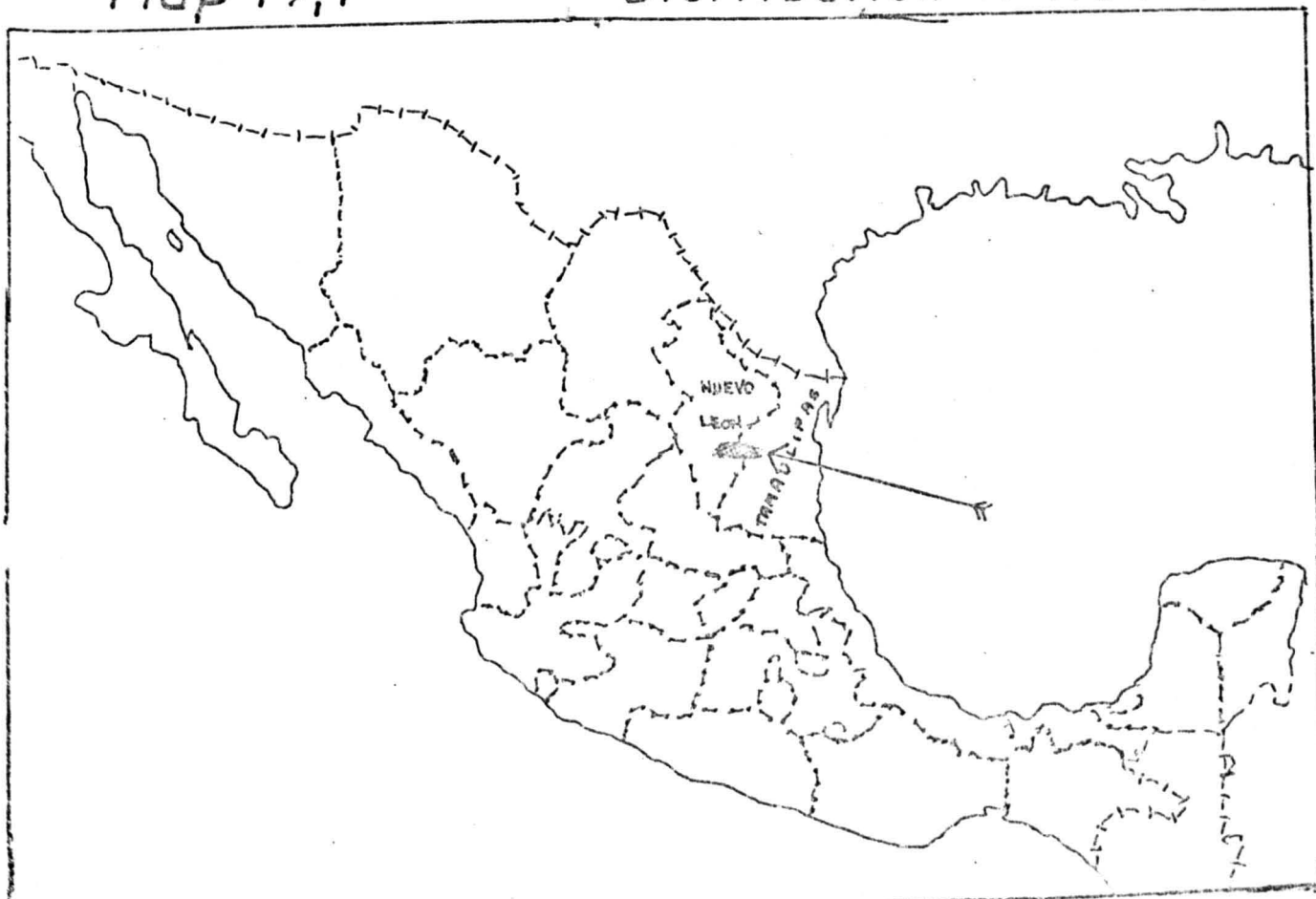
Studies of morphology and palynology both strongly suggest that the nearest allies of Paracaryopsis lie in Paracynoglossum. The cordate radical leaves of P. coelestina and P. malabarica, the pilose elevated veins on the lower leaf surface, and the blue or violet corollas are all characters found in the latter genus, although not all in one species. However, Paracaryopsis, particularly P. lambertiana, differs strongly from Paracynoglossum in the form of the nutlets. The multi-veined calyx is another useful differential (but not diagnostic) character. The pollen resembles that of Paracynoglossum sect. Latifolia in its usually strong constriction but is on the whole more highly derived, the culmination being P. lambertiana. Paracaryopsis probably represents the result of

a Paracynoglossum type ancestor, which probably resembled P. meeboldii or P. ritchiei, evolving winged nutlets and diversifying. Within the genus, P. coelestina and P. malabarica are very closely allied, sharing many common characters; P. lambertiana is more distantly related, differing in several important characters e.g. leaf shape and nutlet morphology.

Map 18,1 Distribution of Paracaryopsis



Map 19,1 Distribution of Madrea



CHAPTER 19

11. MADREA R. Mill

19.1 INTRODUCTION

It has been demonstrated above (sects. 2.5.1, 2.5.3) that the genus Omphalodes as currently circumscribed is heterogeneous, comprising four distinct, unrelated elements, three of which are excluded from the genus as here defined. The new genus Madrea, proposed here, represents one such segregate. Its single species, M. erecta, is endemic to the Sierra Madre Oriental in the provinces of Nuevo Leon and Tamaulipas in northern Mexico (Map 19.1) where it inhabits steep valleys and ravines in oakwoods at an altitude of 1500-2000 m.

19.2 SYSTEMATIC TREATMENT

Madrea R. Mill, gen. nov.

A generibus Omphalode atque Cynoglosso nucula late alata, ala planissima, laevissima (genus Paracaryum in mentem revocans), corolla lobis sinubus indistincte plicatis differt; ab omnibus speciebus Mimophyti caule stricto erecto, foliis lanceolatis basi non cordato, nucula maiore late planoalata margine integri valde distinguitur.

Herba perennis erecta foliis discoloribus subtus ± subcinereis, pilis mollibus arcuatis brevibus, caulibus pilosis infra glabrescentibus, inflorescentia primum dense circinnato, demum pseudoracemosa secunda valde elongata, ebracteata, simplice vel furcata. Calyx parvus fere usque ad basin 5-partitus, lobis inaequalibus lanceolatis acutis, in statu fructifero subreflexis paulo elongatis. Corolla breviter campanulata usque ad subrotata tubo brevi, limbo patente ad medium vel ultra lobata, lobis rotundis, sinubus indistincte plicatulis; fornices trapeziformes apice emarginato papilloso; filamenta ad medium tubi inserta, brevissima; antherae oblongae inclusae, apicibus usque ad bases fornicium vix attingentibus.

Figure 19.1

Madrea erecta: Morphology (All drawn from Meyer & Rogers 2890)

1 Middle cauline leaf, x 0.87

2 Lower surface of leaf: indumentum, x 8.7

3 Trichome from lower surface of leaf, x 35

4 Upper surface of leaf: indumentum, x 8.7

5 Trichome from upper surface of leaf, x 35

6 Inflorescence, x 0.45

7 Stem indumentum, x 6

8 Inflorescence indumentum, x 4.4

9 Calyx and style, x 8.7

10 Corolla opened out, x 8.7

11 Dorsal surface of nutlet showing obcampanulate stigma, x 8.7

Figure 19,1

Stylus florifer calycem vix aequilongus, fructifer alongatus nucula longior. Ovarium 4-ovulatus. Nucula una tantum evoluta (3 abortae) minute tenuipilosa, ala plana non incurvata margine integerrimo vel obsolete denticulato, disco convexo laevo vix carinato obsitae. - Species unica Novam Hispaniam septentrionalem habitat. - Nomen derivatur a montibus 'Sierra Madre Oriental' ubi crescit.

Typus generis: Madrea erecta (I.M. Johnston) R. Mill.

Differs from Omphalodes and Cynoglossum by its broadly winged nutlets, wing flat, smooth (reminiscent of that of Paracaryum), corolla with indistinctly plicate lobes; readily distinguished from all species of Mimophytum by the strictly erect stem, lanceolate leaves not cordate at base, and by larger nutlets with broad flat entire wing.

Perennial erect herb with discolorous leaves ± greyish beneath with soft short curled hairs, stems pilose, glabrescent beneath; inflorescence densely circinnate at first, then greatly elongate, pseudoracemose, secund, ebracteate, simple or furcate. Calyx small, divided almost to base into 5 unequal lanceolate acute lobes, slightly accrescent in fruit with lobes becoming subreflexed. Corolla shortly campanulate to subrotate, tube short, limb patent, lobed to middle or deeper, lobes rounded, with indistinctly plicate sinuses; faucal scales trapeziform, papillose at apex; filaments inserted at middle of tube, very short; anthers oblong, included, their apices scarcely reaching the bases of the scales. Style hardly equalling calyx in flower, elongating and longer than nutlet in fruit. Ovary 4-ovulate. Nutlet solitary by abortion, minutely and thinly pilose, with flat (not incurved) wing with entire or obsoletely denticulate margin, disc convex, smooth, scarcely keeled. - A single species inhabiting northern Mexico.

Madrea erecta (I.M. Johnston) R. Mill, comb. nov. (Fig. 19.1).

Syn: Omphalodes erecta I.M. Johnston in Arn. Arb. 16: 204 (1935).

Perennial herb, stem erect, simple, 30-60 cm, sparsely pilose,

glabrescent especially in lower part. Radical leaves unknown (not developed?). Cauline leaves alternate, lanceolate or broadly lanceolate, 50-110 x 15-30 mm, apex gradually acuminate, base subobtuse to ± cuneate, lower petiolate to 6 mm, upper sessile; all discolorous, upper surface green, drying dark brown-black, lower surface grey; midrib and arcuate lateral veins ±depressed above, slightly elevated on lower surface; upper surface with sparse, antrorsely adpressed, curved, slender hairs arising from conspicuous pustulate bases surrounded by several rows of narrowly oblong, calcarescent subsidiary cells; lower surface pale grey, ± densely pilose, hairs minutely tuberculate at base. Cymes terminal to subterminal, ebracteate, at first densely circinnate, elongating in fruit, ± secund, +densely adpressed-pilose. Pedicels shorter than calyx at anthesis, elongating slightly in fruit. Calyx 4-6 mm long, divided nearly to base, densely grey-strigose, lobes lanceolate, slightly unequal, 3-4 mm long. Corolla ultramarine blue, sometimes with violet centre, 6.5-7 mm, subcampanulate; tube c. ½ length of limb, 2.5-3 mm; limb 4-4.5 mm long, c. 13 mm diam., patent, lobed to middle or beyond; lobes 4-5 mm, rounded, sinuses indistinctly plicate. Faucal scales 1.3 mm, apex subemarginate, papillose. Stamens included, filaments very short, inserted near middle of corolla tube; anthers oblong, their apices situated at or below bases of scales. Style (2-) 3.5 mm, scarcely equalling calyx in flower, elongating to 9 mm in fruit and longer than nutlet; stigma obcampanulate. Nutlet solitary (3 aborting), broadly ovoid, 8 mm diam., minutely and sparsely pilose, with broad spreading entire or minutely denticulate wing; disc smooth, dorsal surface convex with indistinct keel.

19.3 PALYNOLOGY

Pollen heterocolpate; tricolporate, tripseudocolpate, oblong, dumbbell shaped with strong equatorial constriction (C = 78-84); poles in

equatorial view rounded, not angular as in Mimophytum; amb trigonal, appearing ± circular, convex, obtuse. P = 8.8-10.1 μm; E = 4.1-4.5 μm; B = 4.9-5.5 μm; D = 4.8-5.3 μm. P/E = 2.02-2.35, P/B = 1.65-1.84 (prolate). Colpi narrow, ± linear, indistinct (sometimes scarcely visible), bordered by minute bacula; endoaperture a distinct endocolpus; pseudocolpi very narrow, ± linear; collar absent. NPC = 345.

19.4 DISCUSSION

JOHNSTON (1935) in his description of Omphalodes erecta drew attention to the distinctive nature of this species and its lack of relationship with the other Mexican taxa then included in Omphalodes (here referred to Mimophytum). He noted that its habit was more reminiscent of Cynoglossum than Omphalodes (in his sense).

In its discolorous leaves with somewhat camptodromous venation (Fig. 10.1, no. 1) and densely pubescent lower surface (Fig. 19.1, no. 2), Madrea erecta does bear a resemblance to some of the E. Asiatic members of Paracynoglossum as here defined. Comparing the species with European species of Omphalodes, the leaf venation is nearest to that of O. nitida, but in that species, as (more markedly) in other species of Omphalodes, the veins are brochidodromous, i.e. they curve inwards and unite with the vein above.

The strict, somewhat secund ebracteate cyme (Fig. 19.1, no. 6) is also close to that found in Paracynoglossum and differs markedly from the usual bracteate slender cymes of Mimophytum. The plicate sinuses of the corolla lobes are also unknown in Eurasian Omphalodes, but similar, better developed plicate sinuses occur in Mimophytum.

The most distinctive feature of Madrea is the large, solitary nutlet (Fig. 19.1, no. 11) with spreading wing, which is unlike that of any known species of either Cynoglossum or Omphalodes, and is indeed extremely similar

to the winged nutlets of Paracaryum subgen. Modestomattiastrum or Rindera; as in those taxa, it is attached by a nearly apical scar to the rather high gynobase. Pilose nutlets are unknown in either Rindera or Paracaryum, however, and in the majority of species of similar habit in those genera, all four nutlets mature. The inclusion of M. erecta in Rindera is entirely ruled out on grounds of floral morphology and palynology, while the very different vegetative habit, the corolla with plicate lobes, the pilose nutlets, and the unusual obcampanulate stigma (Fig. 19.1, no. 11) preclude its inclusion in Paracaryum. Though obviously related to Cynoglossum, especially perhaps to the Mexican species C. pringlei (which I have not seen), the winged nutlet lacking anchor-like glochidiate spinules delimits Johnston's species from that genus. Hence, I consider the taxon to represent an endemic, monotypic genus, and have named the genus after the mountain range which it inhabits (S. Madre Oriental).

In pollen morphology, M. erecta closely resembles Paracynoglossum. The strongly constricted pollen precludes any relationship with Cynoglossum officinale or its N. American relatives; in this respect, Madrea sharply differs from Cynoglossum, and its recognition at generic rank is supported. It must be emphasised, however, that the palynology of C. pringlei is at present unknown, although Greenman, when describing its morphology, related it to C. officinale.

The equatorial constriction of the pollen of Madrea is weaker than in most species of Mimophytum. Furthermore, in equatorial view the poles of the pollen of all species of Mimophytum appear subangular so that the outline of the pollen more resembles a bow tie than a dumb-bell or hour glass as in Madrea and Paracynoglossum.

From Omphalodes, Madrea differs palynologically by the subtrigonal amb and by the conspicuous development of the endocolpus at the expense of the colpi, which appear almost invisible in some material. The colpi are

bordered by a row of minute bacula, not by continuous muri as in Omphalodes. From the Japanese species formerly grouped in Omphalodes and here segregated as the genus Desmolopha, the pollen differs in the narrower colpi bordered only by bacula; by the stronger equatorial constriction; by its smaller size; and by the much higher values of P/E.

19.5 RELATIONSHIPS

The nearest allies of Madrea appear to be in Cynoglossum and Paracynoglossum. Apart from the shared characters already outlined, the trichomes with pustulate bases which are surrounded by up to 3 concentric rings of subsidiary cells which become calcified with age, are of a type found widely in Cynoglossum and Paracynoglossum, but not at all in either Omphalodes or Mimophytum. In C. pringlei, the unwinged glochidiate nutlet is also said to be solitary by abortion (GREENMAN 1904). The occurrence of nutlet abortion in sympatric taxa closely related at the generic level suggests that in Mexico it may be an adaptive response to the stresses of a largely desertic habitat. However, Madrea appears to be more mesophytic in its ecological requirements than are the species of Mimophytum, preferring streamsides in oakwoods, field borders and waste places.

CHAPTER 20

12. PARACYNOGLOSSUM M. Popov

20.1 INTRODUCTION

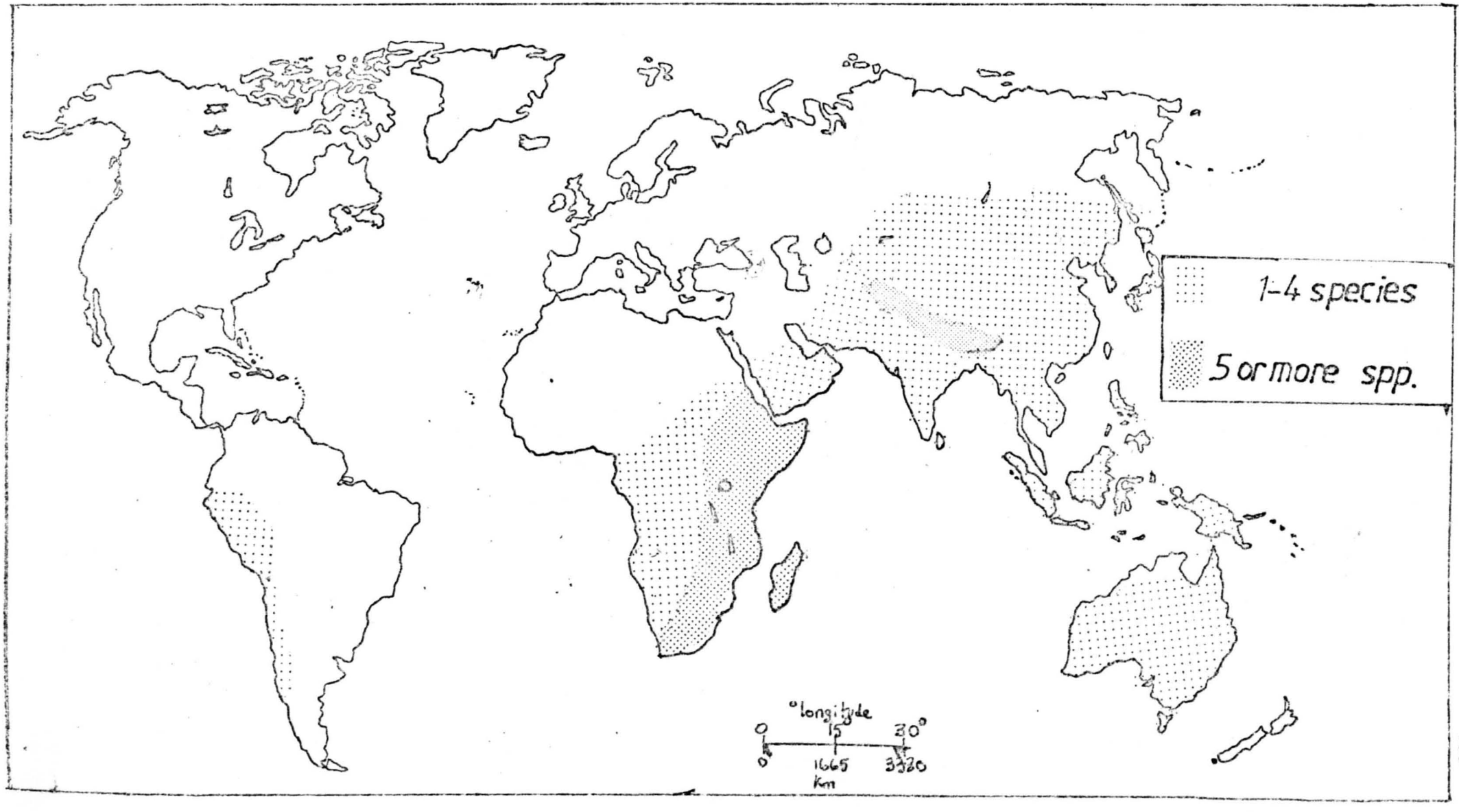
The genus Paracynoglossum as here defined comprises 42 species. It largely replaces Cynoglossum east of the Urals and its species are widely distributed in temperate and tropical Asia east to Japan and New Guinea. Species also occur in Australia and Africa, while three are endemic to S. America (Map 20.1). The genus is absent from Europe (its western limit is N.E. Anatolia) and from N. America.

The genus was separated from Cynoglossum by POPOV (1953) and typified by P. denticulatum (DC.) M. Popov. As delimited by him, the genus included ten species, but only three combinations were validly published. RIEDL (1962) reduced Popov's genus to subgeneric status within Cynoglossum, and considered P. denticulatum to be conspecific with Cynoglossum glochidiatum Wallich. He divided subgen. Paracynoglossum into two sections: sect. Paracynoglossum (13 species) and sect. Axillaria (monotypic: C. latifolium). KAZMI (1971) also treated Cynoglossum in a broad sense, and did not cite the relevant combination in Paracynoglossum in his synonymy of C. glochidiatum.

POPOV (op. cit.) considered the free nutlets an essential character of Paracynoglossum. The same state is found in the African species of Cynoglossum, and as these also resemble Paracynoglossum rather than Cynoglossum s.s. in habit, corolla colour and pollen morphology, I have transferred these to Paracynoglossum in the present treatment. Cynoglossum paniculatum, C. limense and C. trianaeum from S. America also resemble Paracynoglossum in their morphology and palynology and are included in the genus here. Cynoglossum latifolium, which Riedl included in sect. Axillaria of C. subgen. Paracynoglossum, is awarded generic rank in the present treatment as Austrocynoglossum M. Popov ex R. Mill (Chapter 23), but the remaining three Australian species are included in Paracynoglossum.

Map 20,1

Distribution of Paracynoglossum



Accepted Taxa:

P. aequinoctiale (T.C.E. Fries) R. Mill

P. afrocaeruleum R. Mill

P. alpestre (Ohwi) R. Mill (n.v.)

P. amabile (Stapf & Drumm.) R. Mill

P. amplifolium (Hochst.) R. Mill

P. asperrimum (Nakai) M. Popov

P. australe (R. Br.) R. Mill

P. austro-africanum (Weimar ex) R. Mill

P. basuticum (Weimar ex) R. Mill

P. borbonicum (Lam.) R. Mill

P. celebicum (Brand) R. Mill (n.v.: type destroyed?)

P. cernuum (Baker) R. Mill

P. densefoliatum (Chiovenda) R. Mill

P. discolor (Baker) R. Mill

P. divaricatum (Stephan) R. Mill

P. drummondii (R. Br.) R. Mill

P. flexuosum (Brand) R. Mill (n.v.: type destroyed?)

P. formosanum (Nakai) R. Mill (n.v.)

P. geometricum (Baker & C.H. Wright) R. Mill

P. glochidiatum (Wallich) R. Mill

P. hellwigii (Brand) R. Mill (n.v.: type destroyed?)

P. hispidum (Thunb.) R. Mill

P. imeretinum (Kusn.) M. Popov

P. javanicum (Thunb.) R. Mill

P. lanceolatum (Forsskål) R. Mill

P. limense (Willd.) R. Mill

P. meeboldii (Brand) R. Mill

P. microglochin (Bentham) R. Mill

P. monophlebium (Baker) R. Mill

P. nervosum (Bentham) R. Mill

P. paniculatum (Poepp.) R. Mill

P. petiolatum (Hooker fil.) R. Mill

P. ritchiei (C.B. Clarke) R. Mill

P. rochelia (A.DC.) R. Mill

P. schlagintweitii (Brand) R. Mill (n.v.: type destroyed?)

P. stewartii (Kazmi) R. Mill

P. suavolens (R. Br.) R. Mill

P. thomsonii (C.B. Clarke) R. Mill

P. trianaeum (Wedd.) R. Mill

P. trollii (Melchior) R. Mill (n.v.)

P. wallichii (G. Don) R. Mill

P. zeylanicum (Vahl) R. Mill

Excluded Taxon:

P. denticulatum (DC.) M. Popov in Fl. URSS 19: 715 (1953)
= P. glochidiatum (Wallich) R. Mill

ADDENDUM

I have recently been shown material collected by Burtt in S. Africa (1977) and by Miller in the Yemen Arab Republic (1978). Among the material from S. Africa are several sheets labelled 'Cynoglossum spelaeum Hilliard & Burtt', which certainly represents a new species. Since the nutlets are free from the style it must be considered a member of Paracynoglossum following the generic limits adopted here, but the necessary combination cannot be made formally here as the name 'C. spelaeum' has not yet been published. However, I have provided illustrations of the corolla and fruit of this species (Figs. 20.1, no. 2; 20.3, no. 6). The drawings are labelled 'P. spelaeum'.

The specimens from Yemen are referable to several species, including P. lanceolatum, P. afrocaeruleum and possibly P. geometricum, and represent extensions of the known ranges of the latter two species. In addition, there are several sheets of a taxon characterised by white corollas with a blue centre, and large marginate densely glochidiate nutlets of up to 5 mm diam., often with a blue-grey tinge. This also seems to represent a new, as yet unnamed species which will be described in a paper in preparation by Miller and myself. Another specimen collected by Lavranos in the Yemen may also represent a new taxon and will be discussed in the same paper.

20.2 SYSTEMATIC TREATMENT

Paracynoglossum M. Popov in Fl. URSS 19: 715 (1953). Syn: Cynoglossum L. subgen. Paracynoglossum (M. Popov) H. Riedl in Öst. Bot. Zeitschr. 109: 392 (1962) pro parte excl. sect. Axillaria H. Riedl.

Type: P. glochidiatum (Wallich) R. Mill (Syn: P. denticulatum (DC.) M. Popov, loc. cit., 1953).

Similar to Cynoglossum but nutlets with the apex free from the style, and not separating from the style by an awn at maturity. Pollen usually dumb-bell shaped.

Perennial, biennial or annual herbs. Rootstock usually producing few or a single fertile flowering stems, rarely plants subcaespitose (P. schlagintweitii). Stems erect, simple or branched especially in upper part, usually fistulose, 20-150 cm, often woody at base, usually hairy, rarely ± glabrous. Radical leaves petiolate, often large, persistent or not; veins several and indistinct, or leaves distinctly 3-veined with the veins elevated on the lower surface, or 1-nerved; cauline usually sessile, similar to radical but smaller. Inflorescence paniculate, geminate or reduced to a single cyme; cymes partly bracteate or wholly ebracteate, scorpioid, greatly elongating in fruit. Calyx 5-lobed to near base (rarely to ¾ or only ½). Corolla small, infundibular, shortly campanulate or almost rotate, 1-6(-10) mm, tube subequalling or shorter than limb. Faucal appendages (scales) subquadrate or semilunar, entire or emarginate, flat or rarely involute, visibly closing the throat, papillose or glabrous. Stamens included; filaments shorter than anthers; anthers borne between or below corolla scales, ovoid, obtuse, very small. Style prismatic, shorter than or equal to calyx, included in corolla. Gynobase ± high-pyramidal. Nutlets (all 4 usually maturing) attached to gynobase by ventro-apical scar, not coherent to style and not carrying away an awn when shed, 1-6(-10) mm long, dorsoventrally compressed, dorsal surface convex to concave, marginate or immarginate, always ± glochidiate, glochids few or dense, either evenly scattered over nutlet surface or confined to dorsal crest and margin.

1. Nutlets marginate ..... Group A

1. Nutlets immarginate, or unknown ..... Group B

Group A

1. Nutlets (3.5-) 4-5 mm

2. Basal leaves to 8 cm incl. petiole, lamina to 4 x 1.5 cm

3. Petioles of lower cauline leaves 3-4 cm; corolla 9-11 mm diam. ..... 2. nervosum

3. Petioles of lower cauline leaves 5–8 cm; corolla 16–18 mm diam. ..... 3. *petiolatum*

2. Basal leaves 6–45 cm incl. petiole, lamina 3–26 x 1–12 cm

4. Basal leaves to 45 cm incl. petiole; lamina to 26 x 12 cm ..... 5. *stewartii*

4. Basal leaves 6–20 cm incl. petiole; lamina not more than 12 x 3 cm

5. Calyx lobes 2 mm; corolla scales semilunar; nutlets glochidiate but not pubescent (Madagascar) ..... 37. *borbonicum*

5. Calyx lobes 3.5–4.5 mm; corolla scales subquadrate; nutlets glochidiate and puberulous or minutely and densely pubescent (Himalayas) ..... 4. *microglochin*

1. Nutlets 1–4 mm

6. Corolla violet-blue with small white spots (*fide* Melchior) ..... 6. *trollii*

6. Corolla pure blue or white *in sicco*, unspotted

7. Corolla white or pale blue

8. Nutlets 1–2(–3) mm

9. Corolla scales semilunar, much broader than long (Africa) ..... 14. *geometricum*

9. Corolla scales subquadrate (India) ..... 29. *ritchiei*

8. Nutlets 3–4 mm

10. Pedicels 7.5 mm in flower, to 11 mm in fruit (Africa: Basutoland) ..... 11. *basuticum*

10. Pedicels 0–2 mm in flower, and fruit (Australia)

11. Corolla scales semilunar (Africa, Arabia) ..... 14. *geometricum*

11. Corolla scales subquadrate or trapeziform (Australia)

12. Disc of nutlet evenly glochidiate ..... 18. *australe*

12. Disc of nutlet smooth or sparsely tuberculate, glochids confined to margin ..... 19. *drummondii*

7. Corolla bright sky- or cobalt-blue when dry (and *in vivo*)

13. Corolla 4–6 mm

14. Stems 30–85 cm high

15. Disc of nutlets with distinct dorsal keel, its glochids mainly confined to this ..... 31. *wallichii*

15. Disc of nutlets lacking dorsal keel, its glochids scattered ..... 24. *amabile*

14. Stems usually more than 1 m high

16. Lateral veins of leaves indistinct, not more densely hairy than lamina; calyx lobes c. 5 mm ..... 7. *thomsonii*

16. Lateral veins of leaves very distinct, more densely hairy than rest of lamina; calyx lobes c. 3 mm ..... 28. *meeboldii*

13. Corolla 2.5–4 mm

17. Hairs of leaves to 0.2 mm, mostly not arising from tuberculate base

18. Leaf veins ± prominently elevated beneath; median leaves 4–6 cm ..... 33. *imeretinum*

18. Leaf veins indistinctly elevated beneath; median leaves to 10 cm ..... 21. *asperrimum*

17. Hairs of leaves longer than 0.2 mm, arising from large conspicuous tuberculate bases (at least on older leaves)

19. Corolla scales subquadrate, as broad as long (Himalayas)

20. Disc of nutlets strongly concave, broadly ovate, glochids scattered; keel inconspicuous; marginal glochids numerous, dilated, confluent, forming broad elevated rim ..... 31. *wallichii*

20. Disc of nutlets weakly concave to slightly convex, glochids confined to ± prominent keel; marginal ones fewer, not or only slightly dilated, rims narrow ..... 32. glochidiatum

19. Corolla scales semilunar, broader than long (Africa)

21. Plant silvery grey-tomentose; leaves densely crowded, broadly obovate-spathulate ..... 13. densefoliatum

21. Plant hispid, not silvery; leaves loosely arranged, often narrow ..... 12. afrocaeruleum

Group B

1. Inflorescence bracteate, at least in lower part

2. Nutlets 4-6 mm diam.

3. Corolla white or pale yellow; nutlets 4-5 mm diam. (Australia) ..... 17. suavolens

3. Corolla blue, purple or brownish; nutlets 5-6 mm diam.

4. Corolla dull purple or brownish (S. Africa) ..... 9. hispidum

4. Corolla blue (Tropical S. America) ..... 42. trianaeum

2. Nutlets 2-3 mm diam.

5. Most flowers subtended by a bract; corolla violet or purple (E. Asia: China, Tibet and adjacent U.S.S.R.) ..... 1. divaricatum

5. Only lowest 1-2 flowers subtended by a bract; corolla white or blue (Madagascar)

6. Tubercles absent at base of leaf trichomes ..... 36. discolor

6. Tubercles present at base of leaf trichomes

7. Leaf tubercles milky-hyaline, not becoming calcified ..... 35. monophlebium

7. Leaf trichomes becoming calcified and opaque white ..... 34. cernuum

1. Inflorescence ebracteate throughout

8. Nutlets 4–6 mm diam.

9. Corolla brownish or purplish ..... 9. hispidum

9. Corolla blue

10. Lamina of cauline leaves 8–16 x 3–8 cm ..... 8. amplifolium

10. Lamina of cauline leaves 3–7 x 0.7–3 cm

11. Basal leaves withered at flowering time

..... 10. austro-africanum

11. Basal leaves present at flowering time, forming a rosette

12. Plant caespitose; nutlets 4 mm

(Tibet) ..... 26. schlagintweitii

12. Plant not caespitose; nutlets 5.5 mm

(Africa) ..... 15. aequinoctiale

8. Nutlets 1–4 mm, or unknown

13. Leaf trichomes arising from tuberculate bases

14. Corolla scales involute

15. All stem hairs directed downwards ..... 20. javanicum

15. Upper stem hairs directed upwards ..... 18. australe

14. Corolla scales not involute

16. Leaf tubercles milky-hyaline, not becoming calcified ..... 35. monophlebium

16. Leaf tubercles becoming opaque white and calcified

17. Leaves apparently 1-veined

18. Corolla bright blue; scales subquadrate or shortly triangular (Madagascar) ..... 34. cernuum

18. Corolla pale blue or white; scales semilunar

19. Calyx lobes 1.5–2 mm (Africa) ..... 16. lanceolatum

19. Calyx lobes 3 mm (Chile) ..... 40. paniculatum

17. Leaves distinctly 3-nerved

20. Calyx veins 1-3, distinct; corolla usually white ..... 39. rochelia

20. Calyx veins indistinct or absent

21. Corolla blue, concolorous ..... 30. zeylanicum

21. Corolla white with blue centre ..... 16. lanceolatum

13. Leaf trichomes not arising from large tuberculate bases though usually from small white bulbous bases

22. Corolla white (sometimes with blue centre)

23. Corolla 4 mm long; scales subquadrate ..... 38. celebicum

23. Corolla 8-9 mm long; scales semilunar ..... 41. limense

22. Corolla entirely blue

24. Stem indumentum sparse, glabrescent below ..... 36. discolor

24. Stem indumentum usually dense

25. Style equal to or longer than calyx in fruit ..... 27. flexuosum

25. Style shorter than calyx in fruit

26. Nutlets 2-3 mm

27. Leaves roughly strigose above ..... 21. asperrimum

27. Leaves strigillose-sericeous above ..... 23. formosanum

26. Nutlets 3-4

28. Stems minutely strigose ..... 25. hellwigii

28. Stems villous or tomentose with long dense often patent hairs ..... 22. alpestre

Sect. Foliata (H. Riedl) R. Mill, comb. nov. Syn: Cynoglossum L. subgen. Cynoglossum sect. Foliata H. Riedl in Öst. Bot. Zeitschr. 109: 392 (1962).

Tall biennial. Rootstock not multicipital, long, thin, vertical, red-brown. Stem simple below, branched above, ± ribbed, adpressed-pubescent. Radical leaves to 15 cm incl. petiole. Cauline leaves all patiolate, stem leafy up to inflorescence. Inflorescence pyramidal-paniculate, with many

branching scorpioid cymes. Cymes bracteate ± throughout. Corolla violet. Scales slightly emarginate. Nutlets immarginate.

Type: P. divaricatum (Stephan) R. Mill - Monotypic.

1. P. divaricatum (Stephan) R. Mill, comb. nov. Syn: Cynoglossum divaricatum Stephan ex Lehm., Asperif. 2: 161 (1818).

The section was referred to Cynoglossum by POPOV (1953) and RIEDL (1962) but its morphology and palynology align it as a member of Paracynoglossum.

Sect. Latifolia R. Mill, sect. nov.

Perennes, 35-150 cm altae. Folia late elliptica vel late ovata, ad basin breviter attenuata vel obtusa vel truncata vel subcordata, venis 5 vel compluribus indistinctis inferne non elevatis provisa; folia basalia longissime petiolata, caulina breviter petiolata suprema sessilia; lamina 6-26 x 1-12 cm. Cymae ebracteatae. Corolla violacea (rarissime albido-maculata) vel intense caerulea, pro genere magna. Nuculae marginatae, 3-6 mm longae.

Perennial, 35-150 cm. Leaves broadly elliptic to broadly ovate, shortly attenuate, obtuse, truncate or subcordate at base, with 5 or more indistinct lateral veins not elevated beneath; basal with very long petioles to 20 cm, cauline strongly petiolate or sessile; lamina 6-26 x 1-12 cm. Cymes ebracteate. Corolla violet or blue. Nutlets marginate, 3-6 mm.

Type: P. nervosum (Bentham) R. Mill

2. P. nervosum (Bentham) R. Mill, comb. nov. Syn: Cynoglossum nervosum Bentham ex C.B. Clarke in Hooker. fil., Fl. Brit. India 4: 158 (1883).

3. P. petiolatum (Hooker) R. Mill, comb. nov. Syn: Anchusa petiolata Hooker in Bot. Mag. 67: t. 3858 (1841); Cynoglossum petiolatum (Hooker) A. DC. in DC., Prodr. 10: 149 (1846); C. nervosum Bentham ex C.B. Clarke var. petiolatum (Hooker) Kazmi in J. Arn. Arb. 52: 350 (1971).

4. P. microglochin (Bentham) R. Mill, comb. nov. Syn: Cynoglossum microglochin Bentham in Royle, Ill. Bot. Himalay. Mount. 1: 305 (1839).

5. P. stewartii (Kazmi) R. Mill, comb. nov. Syn: Cynoglossum stewartii Kazmi in J. Arn. Arb. 52: 350 (1971).

6. P. trollii (Melchior) R. Mill, comb. nov. Syn: Cynoglossum trollii Melchior in Notizbl. Bot. Gart. Mus. Berlin-Dahlem 14: 354 (1939) (n.v.).

7. P. thomsonii (C.B. Clarke) R. Mill, comb. nov. Syn: Paracaryum thomsonii C.B. Clarke in Hooker fil., Fl. Brit. India 4: 161 (1883); Cynoglossum thomsonii (C.B. Clarke) Johnston in Contr. Gray Herb. 73: 72 (1924).

Sect. Amplifolia R. Mill, sect. nov.

Perennis. Caulis crassus basi lignosus. Folia basalia magna, longissime petiolata (petiolum usque ad 30 cm longum), lamina 10-20 x 6-8 cm, cuneata, venis arcuatis subparallelis indistinctis inferne non elevatis. Calyx tantum fere ad medium divisus. Corolla caerulea, 4-6 mm. Nuculae immarginatae, 5-10 mm longae.

Perennial. Stem stout, woody at least at base. Basal leaves long-petiolate (petiole to 30 cm), lamina 10-20 x 6-8 cm, cuneate, with arcuate subparallel ± indistinct veins not elevated beneath. Calyx divided to middle only. Corolla blue, 4-6 mm. Nutlets immarginate, 5-10 mm long. Type: P. amplifolium (Hochst.) R. Mill. - Monotypic.

8. P. amplifolium (Hochst.) R. Mill, comb. nov. Syn: Cynoglossum amplifolium Hochst. ex A. DC., in DC., Prodr. 10: 149 (1846); C. lancifolium Hooker fil. in J. Linn. Soc. (Bot.) 7: 207 (1864).

Sect. Paracynoglossum

Perennial, biennial or annual. Leaves lanceolate to elliptic, often narrow, all or most cauline sessile; veins 1 or usually 3, ± prominently elevated beneath; indumentum usually dense, either evenly distributed over lamina and veins or with the veins much more densely pilose beneath. Calyx divided to base (rarely to $\frac{3}{4}$). Corolla usually intense sky- or cobalt-blue, sometimes white, yellowish or dull purple, 1-5 mm. Nutlets 1-5(-6) mm, marginate or immarginate.

Type: P. glochidiatum (Wallich) R. Mill

9. P. hispidum (Thunb.) R. Mill, comb. nov. Syn: Cynoglossum hispidum Thunb., Prodr. Fl. Capens. 34 (1794).

10. P. austro-africanum (Weimar ex) R. Mill, sp. nov. Syn: Cynoglossum austro-africanum H. Weimar in sched., nom. nud.

Stems to 60 cm, densely white-hispid, hairs retrorse below, antrorsely adpressed above. Basal leaves withered at flowering time; cauline narrowly oblong, acute, c. 45 x 6 mm, lowest attenuate into petiole, upper sessile, cuneate, adpressed to stem, all covered with long slender retrorse trichomes arising from tuberculate bases calcifying with age. Pedicels 1.5-2 mm in flower, increasing to 7 mm in fruit. Calyx 1.5 mm, lobes ovate, antrorsely hispid. Corolla blue, c. 4 mm, tube and limb subequal, limb lobes to c. 0.8 mm. Immature nutlets immarginate, densely covered with long narrow glochids.

Type: South Africa, Transvaal, Wakkerstroom District, Obhoesa, most moist positions particularly streambanks, damp hollows or hillsides, a herb up to 2 ft high, fl. throughout summer, small blue flowers, 1950 m, 18 i 1961, N.J. Devenish 480 (holo. K!).

South Africa: Bechuanaland, Waterfall District, 22 ii 1950, I.B. Pole Evans 77!

11. P. basuticum (Weimar ex) R. Mill, sp. nov. Syn: Cynoglossum basuticum H. Weimar in sched., nom. nud.

Stems thinly hispid below, more roughly patent-hispid above. Basal leaves not seen. Cauline leaves ovate, obtuse, mucronate, to 85 x 26 mm, lower attenuate into petiole to 30 mm, upper sessile, rugose, with trichomes antrorsely adpressed at 45 deg. to midrib, arising from tuberculate bases impressed in small pits, tubercles becoming calcified with age. Pedicels 7.5 mm in flower, increasing to 10.5 mm in fruit. Calyx c. 2 mm, increasing to 3.5 mm in fruit, lobes narrowly ovate, obtuse, densely long white-hispid.

Corolla white. Nutlets 3.5-2.7 mm, strongly marginate, margin markedly raised with short broad-based sometimes incurving glochids; disc almost devoid of glochids, the few present being very small and papilla-like.

Type: South Africa, Cape Province, Molteno District, Broughton nr Molteno, 1920 m, xii 1892, Flanagan 1632 (holo. K!).

12. P. afrocaeruleum R. Mill, nom. nov. Syn: Cynoglossum coeruleum Hochst. ex A. DC. in DC., Prodr. 10: 148 (1846) nom. illegit., non C. caeruleum Buch.-Ham. ex D. Don, Prodr. Fl. Nepal 100 (1825).

13. P. densefoliatum (Chiovenda) R. Mill, comb. nov. Syn: Cynoglossum densefoliatum Chiovenda in Ann. Bot. 9: 82 (1911).

14. P. geometricum (Baker & C.H. Wright) R. Mill, comb. nov. Syn: Cynoglossum geometricum Baker & C.H. Wright in Thiselton-Dyer, Fl. Trop. Afr. 4(2): 52 (1906); C. lanceolatum Forsskål subsp. geometricum (Baker & C.H. Wright) Brand in Engler, Pflanzenreich 78 (IV. 252): 140 (1921); C. mannii Baker & C.H. Wright, loc. cit. (1906).

15. P. aequinoctiale (T.C.E. Fries) R. Mill, comb. nov. Syn: Cynoglossum aequinoctiale T.C.E. Fries in Notizbl. Bot. Gart. Berlin-Dahlem 8: 416 (1923).

16. P. lanceolatum (Forsskål) R. Mill, comb. nov. Syn: Cynoglossum lanceolatum Forsskål, Fl. Aegypt.-Arab. 41 (1775).

17. P. suavolens (R. Br.) R. Mill, comb. nov. Syn: Cynoglossum suavolens R. Br., Prodr. Fl. Nov. Holl. 495 (1810).

18. P. australe (R. Br.) R. Mill, comb. nov. Syn: Cynoglossum australe R. Br., loc. cit. (1810).

19. P. drummondii (Bentham) R. Mill, comb. nov. Syn: Cynoglossum drummondii Bentham, Fl. Austr. 4: 409 (1869); C. australe R. Br. var. drummondii (Bentham) Brand in Engler, Pflanzenreich 78 (IV. 252): 133 (1921).

20. P. javanicum (Thunb. ex Lehm.) R. Mill, comb. nov. Syn: Cynoglossum javanicum Thunb. ex Lehm. in Neue Schr. Nat. Ges. Halle 3(2): 21 (1817);

Myosotis javanica Swartz ex Lehm., loc. cit. (1817).

21. P. asperrimum (Nakai) M. Popov in Fl. URSS 19: 679 (1953).

22. P. alpestre (Ohwi) R. Mill, comb. nov. Syn: Cynoglossum alpestre Ohwi in Acta Phytotax. et Geobot. 1933 (2): 150 (1933) (n.v.).

23. P. formosanum (Nakai) R. Mill, comb. nov. Syn: Cynoglossum formosanum Nakai in Bot. Mag. Tokyo 37: 4 (1923) (n.v.).

24. P. amabile (Stapf & Drumm.) R. Mill, comb. nov. Syn: Cynoglossum amabile Stapf & Drumm. in Kew Bull. 202 (1906).

25. P. hellwigii (Brand) R. Mill, comb. nov. Syn: Cynoglossum hellwigii Brand in Feddes Rep. 13: 546 (1915) (n.v. - type destroyed at Berlin).

26. P. schlagintweitii (Brand) R. Mill, comb. nov. Syn: Adelocaryum schlagintweitii Brand in Feddes Rep. 13: 548 (1915); Cynoglossum schlagintweitii (Brand) Kazmi in J. Arn. Arb. 52: 352 (1971); C. schlagintweitii (Brand) H. Riedl in Öst. Bot. Zeitschr. 119: 70 (1971) comb. illegit. (n.v. - type destroyed at Berlin).

27. P. flexuosum (Brand) R. Mill, comb. nov. Syn: Adelocaryum flexuosum Brand in Feddes Rep. 14: 145 (1915); Cynoglossum flexuosum (Brand) Kazmi, loc. cit. (1971); C. flexuosum (Brand) H. Riedl, loc. cit. (1971) comb. illegit. (n.v. - type destroyed at Berlin).

28. P. meeboldii (Brand) R. Mill, comb. nov. Syn: Cynoglossum meeboldii Brand in Feddes Rep. 14: 323 (1916).

29. P. ritchiei (C.B. Clarke) R. Mill, comb. nov. Syn: Cynoglossum ritchiei C.B. Clarke in Hooker fil., Fl. Brit. India 4: 157 (1883).

30. P. zeylanicum (Vahl ex Hornem.) R. Mill, comb. nov. Syn: Anchusa zeylanica Vahl in herb., ex Hornem., Enum. Hafn. 3 (1807) et Hort. Hafn. 1: 176 (1813) sine descr.; Cynoglossum zeylanicum (Vahl) Thunb. ex Lehm. in Neue Schr. Nat. Ges. Halle 3(2): 20 (1817); Echinospermum zeylanicum (Vahl) Lehm., Asperif. 116 (1818); Myosotis zeylanica (Vahl ex Hornem.) Swartz ex Lehm., loc. cit. (1818); C. furcatum Wallich ex Roxb., Fl. India 2: 6 (1824); C. caeruleum Buch.-Ham. ex D. Don,

Prodr. Fl. Nepal 100 (1825).

31. P. wallichii (G. Don) R. Mill, comb. nov. Syn: Cynoglossum wallichii G. Don, Gen. Syst. Gard. 4: 354 (1838).

32. P. glochidiatum (Wallich) R. Mill, comb. nov. Syn: Cynoglossum glochidiatum Wallich, Cat. 922 (1828); C. denticulatum A. DC. in DC., Prodr. 10: 150 (1846); Paracynoglossum denticulatum (A.DC.) M. Popov in Fl. URSS 19: 674 & 715 (1953).

33. P. imeretinum (Kusn.) M. Popov in Fl. URSS 19: 676 (1953).

34. P. cernuum (Baker) R. Mill, comb. nov. Syn: Cynoglossum cernuum Baker in J. Linn. Soc. (Bot.) 20: 211 (1813).

35. P. monophlebium (Baker) R. Mill, comb. nov. Syn: Cynoglossum monophlebium Baker, loc. cit. (1883).

36. P. discolor (Baker) R. Mill, comb. nov. Syn: Cynoglossum discolor Baker, op. cit. 212 (1883).

37. P. borbonicum (Lam.) R. Mill, comb. nov. Syn: Myosotis borbonica Lam., Tab. Encycl. Bot. 1: 396 (1791); Cynoglossum borbonicum (Lam.) Bory, Voy. Iles d'Afrique 382 (1804); Echinospermum borbonicum (Lam.) Lehm., Asperif. 119, n. 92 (1818); Myosotis strigosa Schlecht. in Ges. Nat. Freunde Berlin Mag. 8: 233 (1818).

38. P. celebicum (Brand) R. Mill, comb. nov. Syn: Cynoglossum celebicum Brand in Engler, Pflanzenreich 78 (IV. 252): 147 (1921) (n.v. - type destroyed in Berlin).

39. P. rochelia (A. DC.) R. Mill, comb. nov. Syn: Cynoglossum rochelia A. DC. in DC., Prodr. 10: 152 (1846); Myosotis lappula Bouton ex DC., loc. cit. (1846).

40. P. paniculatum (Poepp.). R. Mill, comb. nov. Syn: Cynoglossum paniculatum Poepp., Pl. Exsicc. n. 54 diar. no. 225 (1828) et in Hooker & Arnold, Bot. Beechey's Voy. 379 (1830).

Sect. Limenses R. Mill, sect. nov.

Perennes, fortasse scandentes. Caules tenues, angulati, sparse hirsuti vel subglabri. Folia oblonga, acuta vel cuspidata. Cymae laxae ebracteatae vel ad basin foliosae. Corolla alba vel caerulea, cylindrico-infundibuliformis; fornices deorsum semilunares; stamina in medio tubi affixae, antherae non vel vix bases fornicium attingentes. Nuculae 3-6 mm, subglobosae, cicatrice plerumque magna.

Perennial, perhaps scandent. Stems slender, angled, sparingly hairy or subglabrous. Leaves oblong, acute to cuspidate. Cymes lax, ebracteate or leafy at base. Corolla white or blue, cylindrical-infundibular; scales semilunar; stamens inserted in middle of tube. Nutlets 3-6 mm, with large attachment scar.

Type: P. limense (Willd.) R. Mill.

41. P. limense (Willd.) R. Mill, comb. nov. Syn: Cynoglossum limense Willd., Sp. Pl. 1: 762 (1797); C. decurrens Ruiz. & Pav., Fl. Peruv. 2: 6 (1799), incl. var. limense (Willd.) DC., Prodr. 10: 153 (1846).

42. P. trianaeum (Wedd.) R. Mill, comb. nov. Syn: Cynoglossum trianaeum Wedd., Chlor. And. 2: 90, t. 2458 (1859).

20.3 MORPHOLOGY

Paracynoglossum is more variable than Cynoglossum, although many species resemble each other rather closely in facies. Most species can be distinguished from Cynoglossum by eye, but some African ones are closer to Cynoglossum and require dissection of nutlets and corollas to determine the genus.

20.3.1 Rootstock:

Most Paracynoglossum species are biennial, but sect. Latifolia is perennial, as is P. schlagintweitii. The rootstocks of both species of sect. Limenses are also described as perennial. In perennial species, the rootstock is stout, dark and sometimes almost woody, as in P. stewartii.

P. divaricatum, a biennial, has a very long relatively slender red-brown rootstock apparently adapted to xerophily (cf. POPOV, 1953). In most species of sect. Paracynoglossum the root is moderately stout but not so strongly developed as in sect. Latifolia.

20.3.2 Stems:

The stems are always erect (except in sect. Limenses) and may be solitary or few. No species, apart from P. schlagintweitii which I have not seen, is caespitose. Two of the three South American species are unusual in habit; P. trianaeum is said to be stoloniferous although I have not seen stolons in the limited quantity of material available to me, while P. limense is reputedly scandent. Modern material (with field notes) of these species is needed to settle these points since the habit was not apparent from the incomplete material I have seen. The third South American species, P. paniculatum, resembles the tropical Asian species in its biennial habit and erect stem.

The stem may be simple or branched; branches, when present, are frequently long and divaricate. Branched stems are particularly common in the Asiatic species of both sect. Latifolia and sect. Paracynoglossum. The endemic African species more often have simple stems (at least in the vegetative portion), and unbranched stems are also the rule in the two Australian species.

Stem indumentum is variable but usually ± hispid with adpressed to patent hairs or setae. P. cernuum and P. discolor are the only two species to have subglabrous stems, but even in these a few scattered thin hairs are present. Other species, e.g. P. amplifolium, may be glabrescent in the lower part of the stem later.

Of the African species, P. hispidum, P. basuticum and P. austro-africanum have patent-hispid stems; the hairs are etuberculate. P. geometricum, P. densefoliatum and P. afrocaeruleum are adpressed-villous; the indumentum

of P. densefoliatum is particularly dense, almost white-tomentose in some specimens.

The Asian species of sect. Paracynoglossum divide into those with a preponderance of adpressed hairs (P. amabile, P. zeylanicum etc.) and those with mainly patent hairs or setae (P. glochidiatum, P. wallichii, P. asperrimum, P. rochelia etc.). The precise nature of the indumentum has frequently been used to delimit 'species', as by NAKAI (1923) who described Cynoglossum villosulum, C. tosaense etc. As indumentum characters are highly labile, these and similar 'species' are here considered mere variants, unworthy of formal recognition. In the second group the setae may arise from multicellular tuberculate bases; this is also the case in the patent-hispid Australian species P. australe and P. suavolens. In several species, e.g. P.zeylanicum and P. glochidiatum, there are two or more layers of indumentum (as in some species of Paracaryum); patent hairs and/or setae are underlain by adpressed hairs of variable length but shorter than the patent hairs.

Some species of sect. Latifolia show a tendency towards glabrescence. In P. petiolatum, P. nervosum and especially P. microglochin the stems are ± densely covered with ± crisped trichomes but in P. stewartii the stems are sparsely pilose, rarely even glabrous and shining. P. thomsonii is glabrous below but hairy above.

20.3.3 Leaves:

Leaf shape, venation and indumentum are useful in delimiting both formal taxonomic sections and informal groups within the genus. Sect. Latifolia is defined by its ovate to lanceolate cauline leaves, cordate to shortly cuneate at the base, with numerous, usually non-elevated veins. The leaves of this section are often large (radical up to 26 x 12 cm, but usually 6-15 x 2-3 cm). P. microglochin is transitional to sect. Paracynoglossum in having more oblong-lanceolate leaves with the veins ± raised on the lower surface, but the leaf base is shortly cuneate rather than attenuate or amplexicaul.

The Ethiopian and Arabian species P. amplifolium also has large ovate radical leaves similar to those of sect. Latifolia. On account of its different floral morphology, its immarginate (not marginate) nutlets, and the calyx divided only to the middle, it is not included in sect. Latifolia.

Sect. Paracynoglossum is characterised by its oblong-lanceolate to linear-lanceolate leaves, the radical being long-cuneate or attenuate into the petiole, while the cauline are frequently amplexicaul and often borne strictly erect on the stem. The leaves are normally smaller than those of sect. Latifolia, although P. borbonicum is exceptional in having leaves up to c. 20 cm long including the petiole.

Informal groups can be recognised within sect. Paracynoglossum on the basis of leaf venation and indumentum:

1. 'hispidum' group: S. African species (P. austro-africanum, P. basuticum, P. hispidum). - Leaves greyish. Veins 1-several, indistinct, not raised beneath. Indumentum adpressed-hispid, hairs usually arising from calcifying tuberculate bases. P. basuticum is unusual in having somewhat rugose laminas, a character it shares with the S. American species P. trianaeum.
2. 'afrocaeruleum' group: E. African species (P. aequinoctiale, P. geometricum, P. densefoliatum, P. afrocaeruleum). - Leaves greyish to whitish, sometimes dark green. Veins c. 3, distinctly raised beneath. Indumentum densely and evenly adpressed, setose, sericeous or tomentose, not noticeably denser on veins. Tubercles present or absent.
3. 'australe' group: Australian species (P. australe, P. drummondii, P. suavolens). - Leaves greenish or greenish-brown when dry. Vein 1, indistinct, not raised. Indumentum of densely and evenly adpressed strigose setules on both surfaces, trichomes arising from tuberculate bases.
4. 'rochelia' group: Mascarene Islands. (P. rochelia, P. cernuum, P. borbonicum

P. discolor, P. monophlebium). - Leaves dark brown when dry. Veins 1-3, not or scarcely raised beneath. Indumentum of setules arising from tuberculate bases (P. rochelia, P. borbonicum, P. monophlebium) or sparsely hispid or glabrous above, glabrous or white-canescent beneath (P. cernuum, P. discolor).

5. 'glochidiatum' group: Himalayas, India and E. Asia, E. to western S. America (P. paniculatum), also S. to E. Africa (P. lanceolatum). (P. amabile, P. asperrimum, P. hellwigii, P. alpestre, P. formosanum, P. celebicum, P. javanicum, P. paniculatum, P. imeretinum, P. glochidiatum, P. wallichii, P. meeboldii, P. zeylanicum, P. lanceolatum). - Leaves dark brown to green when dry. Veins several, lateral ones arising pinnately from midrib but arcuately camptodromous to form 2 distinct undulating submarginal veins, all prominently raised beneath. Indumentum variable in quality, but hairs always very much denser on the the lower surface along the veins than on the lamina surface. Upper surface shortly adpressed-strigillose or -villosulous, (P. amabile etc.) to long-setulose (P. glochidiatum and P. wallichii).

P. divaricatum (Sect. Foliata) is unique in the genus in having all cauline leaves petiolate. The radical leaves are oblong-lanceolate, the cauline lanceolate. BRAND (1921) and POPOV (1953) disagree as to the indumentum of this species. Brand described the upper surface as glabrous and green, the lower as greyish-pubescent, while Popov said that the leaves are covered with moderately dense grey down. The specimens I examined at Kew (Wang 503, Hsia 2924) both had dense pubescence on both surfaces. The hairs were short and adpressed, arising from multicellular tuberculate bases on the lower surface and from small tubercles on the upper. It would seem therefore that Popov's description is the more accurate, although it is possible that the density of indumentum on the upper surface is variable.

The two S. American species which I have classified in sect. Limenses are distinct in their leaf morphology. Both species have very acute,

often even cuspidate leaf apices, a character rare elsewhere in the genus and mainly confined to sect. Latifolia. P. trianaeum is unusual in the genus in having the upper surface of the lamina rugulose; any hairs are confined to its apical half. The lower surface is densely strigose and greyish. P. limense is characterised by its very thin membranous sub-decurrent leaves which are sparingly hairy above and densely hairy beneath. In both species the 3-5 veins are rather indistinct and not raised on the lower surface.

20.3.4 Inflorescence:

The 'primitive' inflorescence type in Paracynoglossum appears to be a much branched panicle of greatly elongating scorpioid cymes, as found in P. divaricatum and many species of sect. Paracynoglossum and sect. Latifolia, e.g. P. lanceolatum, P. amabile, P. nervosum and P. glochidiatum. In other species, however, this is reduced to a terminal 2-3-geminate cyme with sometimes 1-3 lateral cymes immediately below, as in P. borbonicum, while in some species (e.g. P. limense) the inflorescence is reduced to a single terminal cyme which may be geminate or not.

The inflorescence may be bracteate or ebracteate. Conspicuously bracteate cymes occur in P. divaricatum and P. suavolens, while P. amplifolium and some species from Madagascar (e.g. P. discolor, P. cernuum and P. monophlebium) are bracteate only at the base of the inflorescence. P. trianaeum is unique in the genus in having extremely lax cymes, the lower flowers of which are remote and subtended by relatively large leaf-like bracts; in the other species listed above, the bracts are ± distinct from the leaves (except in P. divaricatum) and much smaller than them. P. trianaeum appears to have developed along similar lines to Austrocynoglossum latifolium (Chapter 23), but the flowers are truly axillary rather than arising below the bracts as in that species. All other species are ebracteate.

Species differ in the degree of elongation of the cymes and the number and density of the flowers and fruits. Many-flowered, dense inflorescences

prevail in sect. Paracynoglossum, e.g. P. zeylanicum, P. glochidiatum and P. lanceolatum, but in P. amabile and its allies and in the P. rochelia group the inflorescence is more lax. Lax inflorescences also occur in P. hispidum and some other African species (but not P. afrocaeruleum), and in P. suavolens.

20.3.5 Pedicels:

Pedicel length is very variable. The longest are probably those of P. trianaeum, which at 10-20 mm are 2-3 times as long as the calyx even at anthesis, and P. divaricatum, which has pedicels up to 3 cm. P. amplifolium has pedicels up to 11 mm at anthesis, while in P. basuticum, P. suavolens and P. hispidum they are 4-7 mm at flowering time. Most species of sects. Paracynoglossum and Latifolia are characterised by their very short pedicels, 0.5-4 mm at anthesis.

The pedicels are patent or upwardly directed in most species (at anthesis), but in some (e.g. P. cernuum, P. trianaeum) they are recurved and nodding, even at anthesis. In some other species the flowering pedicels are suberect, becoming arcuate or even hamately recurved in fruit, e.g. P. zeylanicum and P. suavolens.

The degree of elongation after anthesis is variable. Most species show about a 100% increase in length, but P. austro-africanum is notable for its pedicels which elongate from less than 2 mm at flowering to 7 mm in fruit; P. hispidum shows a similar percentage increase from 4-6 mm to 14 mm or more. On the other hand, P. basuticum showed a relatively small increase of 40% from 7.5 to 10.5 mm in the specimen examined.

20.3.6 Calyx:

The calyx is always equally 5-lobed and although there is some accrescence in fruit this is not normally more than 100-150%. This combination of characters distinguishes Paracynoglossum from Ivanjohnstonia.

In practically all species the calyx is divided almost to the base. The only exceptions are P. stewartii and P. microglochin of sect. Latifolia,

Figure 20.1

Paracynoglossum: Corolla Morphology

(All drawings are of opened out corollas)

1 P. hispidum, x 8.7 (H.H. Johnston 173)

2 'P. speleaeum', x 8.7 (Hilliard & Burtt 10104)

3 P. amplifolium, x 8.7 (Scheffler 237)

4 P. afrocaeruleum, x 8.7 (Coady K43)

5 P. geometricum, x 8.7 (Swarbrick 2358)

6 P. lanceolatum, x 8.7 (Cooper 3589b)

7 P. glochidiatum, x 8.7 (Podlech 12627)

8 P. wallichii, x 4.4 (Lace 3401)

9 P. zeylanicum, x 4.4 (Stainton 464)

10 P. amabile, x 4.4 (Stainton, Sykes & Williams 8808)

11 P. javanicum, x 4.4 (Cruttwell 751)

12 P. rochelia, x 4.4 (Johnston 5 xii 1888)

13 P. limense, x 4.4 (Beechey s.n.)

14 P. australe, x 4.4 (Jackson 478)

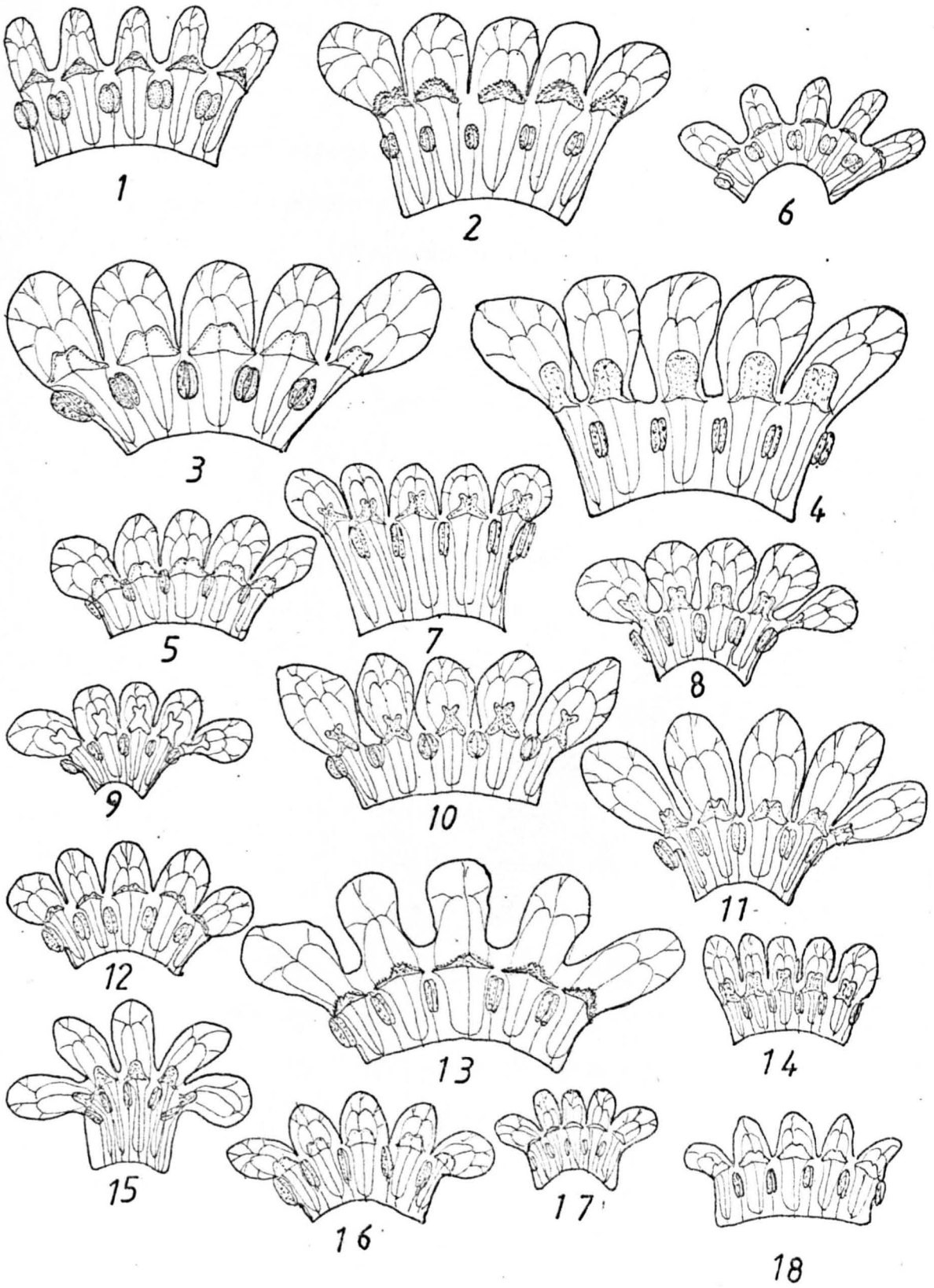
15 P. discolor, x 4.4 (Baron 1828)

16 P. suavolens, x 4.4 (Morrison 23 xi 1889)

17 P. paniculatum, x 4.4 (Fiebrig 2476)

18 P. trianaeum, x 8.7 (Spruce 5554)

Figure 20,1



in which it is divided to 4/5; P. zeylanicum (¾); and P. amplifolium, which is unique in the genus in having the calyx divided only to the middle.

In most species the calyx lobes are ovate; this condition prevails practically throughout sect. Paracynoglossum except for P. wallichii (oblong) and P. rochelia and P. monophlebium (oblong-elliptic). Most species of sect. Latifolia, however, have oblong-ovate lobes while in P. divaricatum, P. schlagintweitii, P. flexuosum, P. limense and P. trianaeum they are oblong to elliptic.

Calyx indumentum is variable, but broadly similar to that of the leaves. The hairs may be adpressed (strigillose, villosulous, sericeous or even tomentose) or patent and setulose, but are always antrorse.

20.3.7 Corolla (Figures 20.1, 20.2):

The corolla in Paracynoglossum is campanulate to infundibular-cylindrical. There is relatively little variation in shape throughout the genus. The tube is normally subequal to or very slightly longer than the limb; only in P. limense (Fig. 20.1, no. 13) is it somewhat elongate, while in the P. amabile group it tends to be reduced and noticeably shorter than the limb.

The largest corollas are those of sect. Limenses (8-9 mm) and most of sect. Latifolia (7-9 mm long, up to 16 mm diam. in P. nervosum). P. trollii of the latter section has smaller corollas but at 4-5 mm these are still larger than in most other species. Other species with relatively large corollas are P. amplifolium (Fig. 20.1, no. 3) (4.5-5.5 mm) and P. suavolens (5-6 mm). The majority of species have corollas 2-4 mm long; those of P. lanceolatum (Fig. 20.1, no. 6) can be as small as 1.5 mm.

The predominant corolla colour in the genus is bright, deep sky- or cobalt blue. Practically all Himalayan and African species of sect. Paracynoglossum have blue corollas. In P. lanceolatum, however, and several species of the P. rochelia group, the corolla is white (sometimes with a pale blue tinge). White corollas are also characteristic of

P. limense (Fig. 20.1, no. 13), P. suavolens (Fig. 20.1, no. 16) and P. basuticum. P. divaricatum (Fig. 20.2, no. 10) has small violet corollas. The much larger ones of sect. Latifolia are also violet or blue-violet, except in P. nervosum and P. petiolatum (blue). P. trollii is said to have violet lobes with white spots (MELCHIOR 1939); if this is true it is the only species of the Cynoglosseae to have spotted corolla lobes. P. hispidum (Fig. 20.1, no. 1) is also unique in Paracynoglossum in having dull brownish red corollas similar in colour to Cynoglossum officinale.

In nearly all species the corolla scales are subquadrate, ± equal in height and breadth or slightly broader at the base. The apical part is often papillate and the apex is usually at least slightly emarginate. Several species are characterised by their low-triangular to semi-lunar scales much broader than high; it is assumed that this represents a derived type by atavism (see sect.2.3). Species with this type of scale include P. rochelia (Fig. 20.1, no. 12), P. borbonicum, P. lanceolatum (Fig. 20.1, no. 6), P. schlagintweitii and all three South American species (Fig. 20.1, nos. 13, 17, 18).

The stamens are included in the middle of the tube in all species and the anthers are borne at or below the level of the scale bases. In the P. glochidiatum and P. amabile group (Fig. 20.1, nos. 7-10) the anther apices normally just surpass the scale bases but in P. lanceolatum, P. amplifolium and others they are situated distinctly below them.

The largest anthers are those of sect. Latifolia (Fig. 20.2, nos. 11-14), where they may be 1.5 mm or more in length and tend to be oblong, although P. microglochin (no. 11) differs from the others by its small ovoid anthers. In sect. Paracynoglossum they are ovate or broadly ovate, and 0.4-0.8(-1.3) x c. 0.3-0.5 mm.

The style is always short and never exserted from the corolla. The longest styles are those of sect. Limenses (c. 4 mm) and sect. Latifolia (2.5-3 mm). Throughout sect. Paracynoglossum the style is normally

Figure 20.2

Paracynoglossum: Corolla and Nutlet Morphology

(1-9: Dorsal views of nutlets, all x 8.7; 10-14: corollas opened out, x 4.4)

1 P. asperrimum (Taquet 1139)

2 P. amabile (E.E. Maire 1496)

3 P. rochelia (Baron 64)

4 P. borbonicum (Balfour s.n.)

5 P. cf. amplifolium (Lavranos 15937)

6 P. australe (Jackson 478)

7 P. drummondii (Whibley 930)

8 P. suavolens (Morrison 22 xii 1892)

9 P. paniculatum (Fiebrig 3174)

10 P. divaricatum (Bodinier 208)

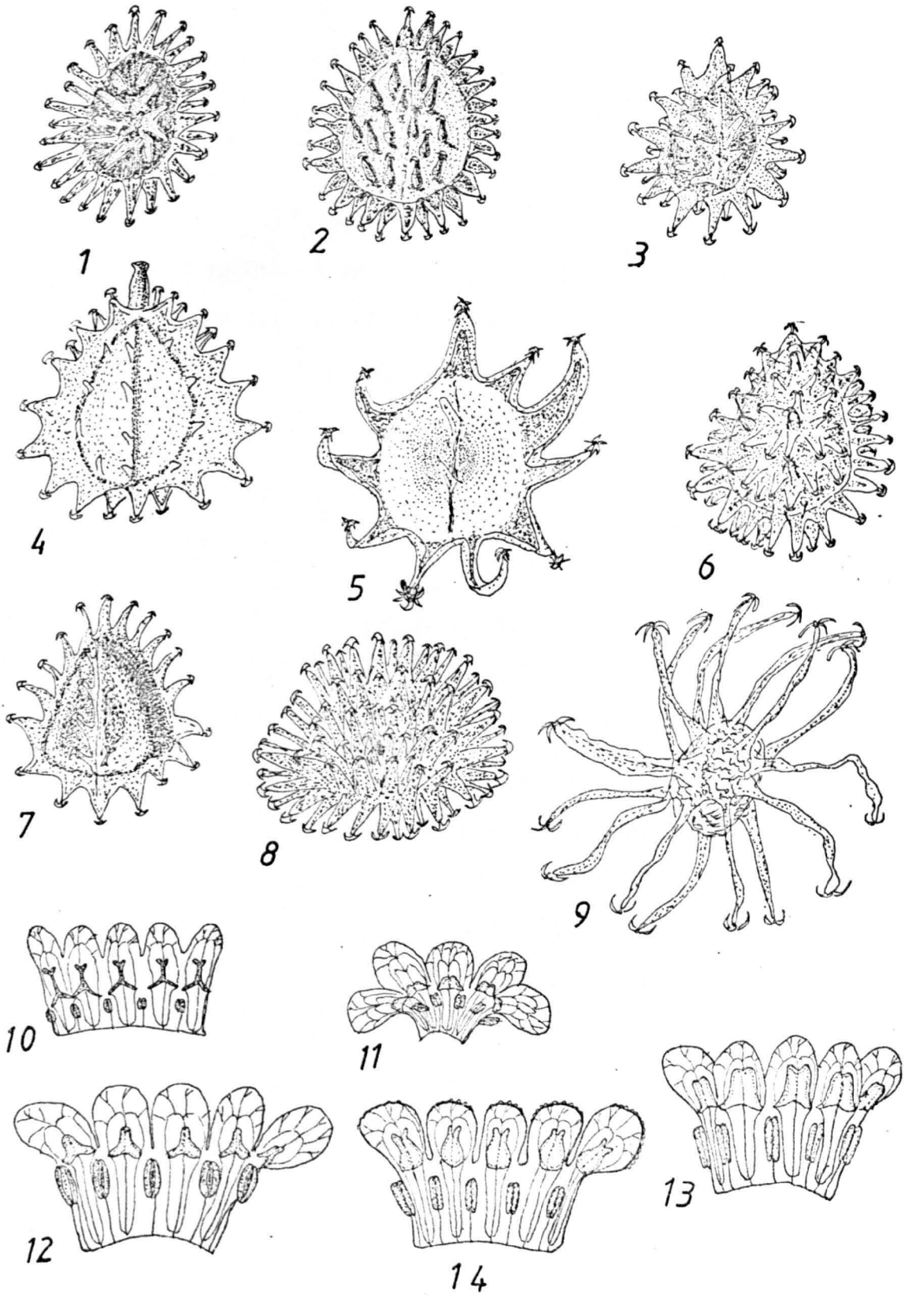
11 P. microglochin (Lace 7929)

12 P. petiolatum (Drummond 14021)

13 P. nervosum (Drummond 1335)

14 P. stewartii (Burtt 877)

Figure 20,2



considerably less than 1 mm at anthesis and often less than 0.5 mm. The shortest style is that of P. lanceolatum (c. 0.2 mm).

20.3.8 Nutlets (Figures 20.2, 20.3):

The genus Paracynoglossum is separated from Cynoglossum by the nutlets being free from the style (though appearing coherent in many species of sect. Paracynoglossum) and not carrying away an awn at maturity.

The nutlets are attached to the pyramidal gynobase by a ventro-apical attachment scar. In most species this is small and triangular, but in sect. Latifolia it is usually large and oblong-ovoid. Very large attachment scars, occupying practically the whole of the ventral surface, are also characteristic of the S. American species P. trianaeum, and P. paniculatum. In a few species, e.g. P. rochelia, P. monophlebium, P. suavolens and P. amplifolium, the attachment scar is borne at the apex of the funicle. All four nutlets usually mature, although 2 are said to be normally abortive in P. schlagintweitii.

The genus is characterised by small nutlets not exceeding 6 mm in diameter, except rarely in P. amplifolium (to 10 mm). The largest nutlets are those of P. trianaeum, P. amplifolium, P. hispidum, P. aequinoctiale and P. divaricatum (5-6 mm). In the species of sect. Latifolia the nutlets are normally 4-5 mm diam., but only 3 mm in P. trollii. All other species have nutlets (1-)2-4(-5) mm, the smallest being those of P. lanceolatum. As in Cynoglossum, the nutlets may be marginate or immarginate. All species of sect. Latifolia (Fig. 20.3, nos. 1-3) have marginate nutlets, as do those of the P. glochidiatum group (Fig. 20.3, nos. 11-15); the P. afrocaeruleum group (Fig. 20.3, nos. 7, 8), P. borbonicum (Fig. 20.2, no. 4), P. australe (Fig. 20.2, no. 6), P. drummondii (Fig. 20.2, no. 7), P. amabile (Fig. 20.2, no. 2) and some forms of P. asperrimum (Fig. 20.2, no. 1), although NAKAI (1923) originally described the latter species as having immarginate nutlets. Immarginate nutlets are characteristic of most other members of the P. amabile group (e.g. P. formosanum) and of P. divaricatum (Fig. 20.3, no.4),

Figure 20.3

Paracynoglossum: Nutlet Morphology (ii)

(All drawings are of dorsal views of nutlets, x 8.7)

1 P. thomsonii (R.R. Stewart 6770)

2 P. nervosum (Drummond 1335)

3 P. microglochin (Watt 7929)

4 P. divaricatum (Mary Clemens 1930)

5 P. hispidum (Hilliard & Burtt 9818)

6 'P. spelaeum' (Hilliard & Burtt 10120)

7 P. afrocaeruleum (Pearson ii 1934)

8 P. geometricum (Swarbrick 2558)

9 P. lanceolatum (Cooper 3589b)

10 P. austro-africanum (Hilliard & Burtt 9614)

11 P. imeretinum (Tong 507)

12 P. glochidiatum (Podlech 12627)

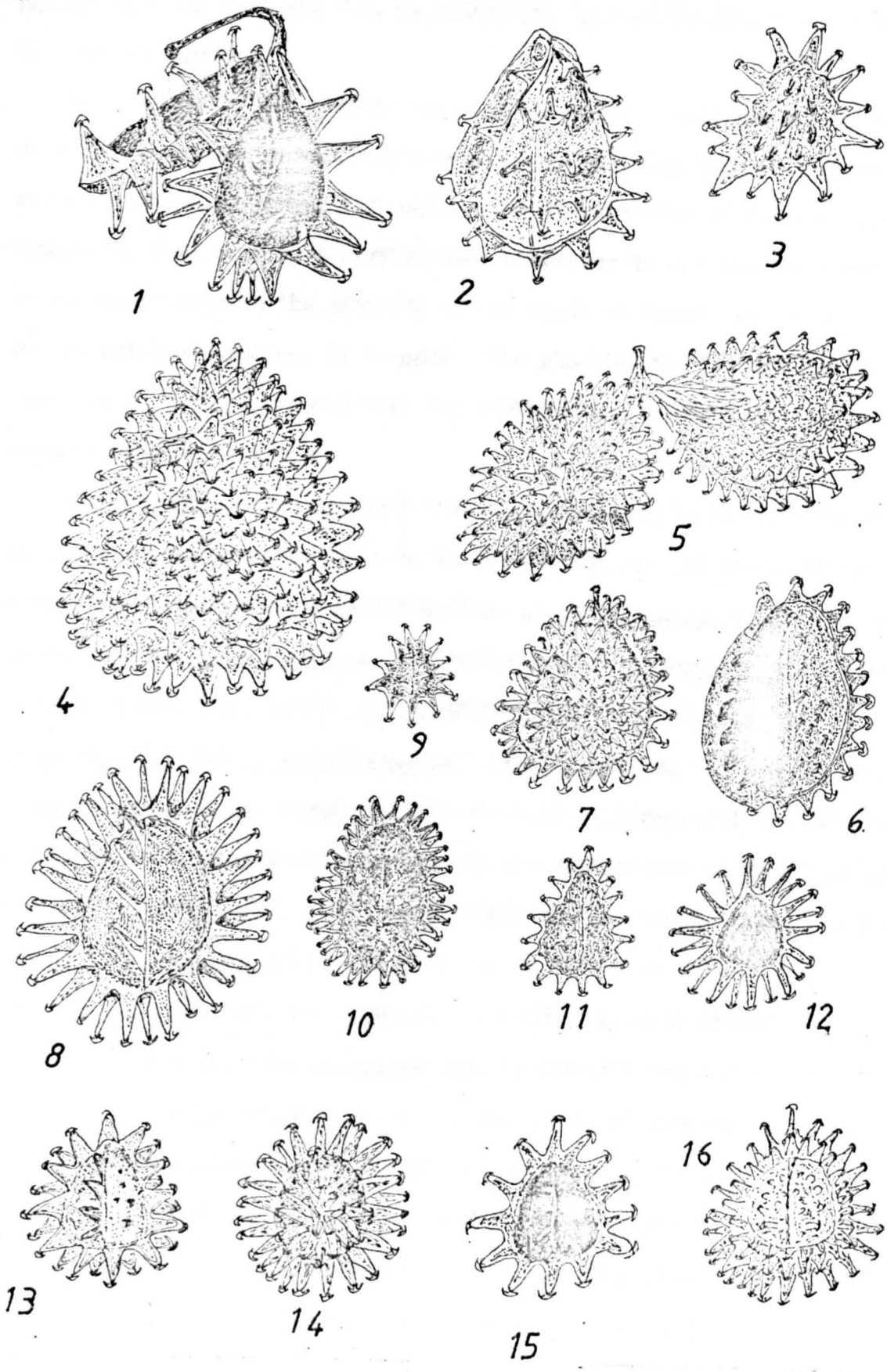
13 P. wallichii (Lace 3401)

14 P. ritchiei (Ritchie 493)

15 P. zeylanicum (W.P. Fang 5723)

16 P. javanicum (Cruttwell 754)

Figure 20,3



P. javanicum (Fig. 20.3, no. 16), P. suavolens (Fig. 20.2, no. 8), P. schlagintweitii, P. flexuosum, P. hispidum (Fig. 20.3, no. 5), P. austro-africanum (Fig. 20.3 no. 10), P. celebicum, P. amplifolium, and all the S. American species.

In all species the nutlets are ± glochidiate. Glochids may be present on both dorsal and ventral surfaces (e.g. P. glochidiatum) or only on the dorsal surface and margin (if any). The distribution of the glochids has frequently been used as a differential character to distinguish species. In marginate species the glochids may be equal in length on margin and disc, or the marginal ones may be longer. The glochids on the disc may be few or dense, evenly scattered over its surface or ± confined to a raised central longitudinal keel.

P. geometricum was separated from P. lanceolatum by BAKER & WRIGHT (1906) by the glochids being confined to the margin and central keel, rather than evenly scattered over the nutlet surface as in P. lanceolatum. BRAND (1921) reduced P. geometricum to a subspecies of P. lanceolatum. Most African floras, e.g. AGNEW (1974), ROBYNS (1948-55), however, treat P. geometricum and P. lanceolatum as distinct species. Since the nutlets of P. geometricum are marginate like those of P. afrocaeruleum, and since its floral and palynological characters are much closer to P. afrocaeruleum than to P. lanceolatum, I follow the trend set by recent African floras and treat P. geometricum at specific rank. There would seem to be ecological justification for this view; ROBYNS (op. cit.) states that in the Albert National Park P. geometricum is nitrophilous and prefers humid habitats, while P. lanceolatum is a pioneer ruderal species.

P. drummondii was separated from P. australe by BENTHAM (1869) by its nutlets with glochids confined to a central keel or absent altogether, rather than densely scattered over the disc as in P. australe, and by its longer, looser indumentum and longer pedicels. BRAND (1921) reduced

P. drummondii to varietal rank under P. australe. Since the two taxa have been found to differ palynologically in addition to the differences noted by Bentham, I prefer to recognise P. drummondii at specific rank.

20.4 PALYNOLOGY

AVETISIAN (1956) examined the pollen of two species of Paracynoglossum (P. glochidiatum and P. imeretinum) and found the grains to be small and dumb-bell shaped. BARBIER & MATHEZ (1973) studied 8 species which are here assigned to Paracynoglossum, and referred them all to their pollen type C (dumb-bell shaped) but commented that they doubted whether C. coeruleum and C. australe were correctly placed in that pollen type. P. alpestre was studied by HUANG (1972), and again the pollen was found to be heterocolpate, subprolate to prolate, with an equatorial constriction.

I have examined pollen from 32 of the 42 species of Paracynoglossum recognised here; quantitative data are summarised in Table 20.1.

20.4.1 Description:

Pollen usually small (P not exceeding 15 μm), elliptic, oblong or usually dumb-bell shaped, equatorial constriction usually present, very weak to very strong (C = 100-70), sometimes absent; heterocolpate, tricolporate, tripseudocolpate. Amb hexagonal, straight or convex, equilateral or anisolateral, acute or obtuse, usually appearing ± peritreme, pseudoapertures included. P = 7-15 μm, E = 3-11 μm, B = 3.5-11 μm, D = 3.5-12 μm. P/E = c. 1.30-2.30, P/B = 1.40-2.00 in constricted grains (pollen usually prolate, sometimes subprolate, rarely almost perprolate). Colpi rhombic or more often ± linear, bordered by bacula and furrow or by furrow only. Endoaperture a lalongate elliptic endocolpus or an endoporus, always simple. Pseudocolpi narrowly rhombic to linear. Collar present (sometimes incomplete) or usually absent. NPC = 3:4:5. Sexine usually smooth.

1. P/E ratio = 1.80-2.30

2. Pollen 11-14 x 6-7 μm ..... 7. 'amplifolium'-type

2. Pollen 6.5-10.5 x 2.5-6 µm

3. Pollen bordered by bacula and furrow

4. Amb equilateral; colpi ± linear;

P/E = 1.90-2.00 ..... 11. '*rochelia*' - type

4. Amb anisolateral; colpi narrowly rhombic;

P/E = c. 2.30 ..... 13. '*limense*' - type

3. Colpi bordered by furrow only

5. Equatorial constriction weak to

moderate (C = 93-86)..... 9. '*glochidiatum*' - type

5. Equatorial constriction strong or very

strong (C = 84-70) .....10. '*nervosum*' - type

1. P/E ratio = 1.30-1.70

6. D = 9-12 µm

7. Pollen elliptic to oblong, not contricted

at equator ..... 1. '*hispidum*' - type

7. Pollen dumb-bell shaped, with equatorial constriction

8. Amb equilateral; D = 10-11.5 µm ..... 4. '*suavolens*' - type

8. Amb anisolateral; D = 8.5-10 µm .....12. '*trianaeum*' - type

6. D = 4.5-9 µm

9. Colpi narrowly elliptic to linear ..... 8. '*javanicum*' - type

9. Colpi narrowly to broadly rhombic

10. Pollen elliptic, not constricted

at equator ..... 2.'*aequinoctiale*' - type

10. Pollen oblong or ± dumb-bell shaped

11. Sexine granular .....5. '*australe*' - type

11. Sexine smooth

12. Pollen apparently binucleate when shed; equatorial

collar present (often incomplete),

sometimes absent ..... 3. '*afrocaeruleum*' - type

12. Pollen trinucleate when shed; equatorial collar absent ..... 6. 'divaricatum' - type

1. 'hispidum' - type

Species included and material examined:

P. hispidum (Thunb.) R. Mill, agg. (S. Africa: Blesbok Flats, 915-1220 m, Drège! Great Vals River, Riversdale District, Burchell 6543! Somerset, Bowker s.n.! Lesotho: Masero Experimental Station, 1525 m, 22 x 1969, Williamson 192!).

Pollen elliptic to oblong, equatorial constriction ± absent. Amb hexagonal, straight or convex, obtuse. P = 11-15.5 µm, E = 7-11 µm, D = 8-11 µm. P/E = c. 1.30-1.80 (subprolate to prolate). Colpi rhombic, bordered by bacula and furrow. Endoaperture a lalongate endocolpus bordered by bacula and/or furrow and sometimes ornamented with surface bacula. Pseudocolpi narrowly rhombic, broadening abruptly at equator, bordered by bacula and furrow. Collar absent. Sexine smooth. Apparently binucleate.

2. 'aequinoctiale' - type

Species included and material examined:

P. aequinoctiale (T.C.E. Fries) R. Mill (Somaliland: Surud, W. of Erigava, 7800 ft., 30 x 1956, P.R.O. Bally 1126a!).

Similar to 'hispidum' - type, but pollen slightly smaller, elliptic. P = 9-10.5 µm, E = 6.5-7 µm, D = 7.5-8.5 µm. P/E = 1.40 (prolate). Colpi broadly rhombic. Pseudocolpi broadening abruptly at equator. Collar present.

3. 'afrocaeruleum' - type

Species included and material examined:

P. afrocaeruleum R. Mill (Ethiopia: Wuchacha 'Martaneh', Coady K 43!).

P. densefoliatum (Chiovenda) R. Mill (Ethiopia: Hawer, 14 x 1957, P.E. Ellis 249!).

P. geometricum (Baker & C.H. Wright) R. Mill (Ethiopia: Entotto, Coady K 39!).

P. basuticum (Weimar ex) R. Mill (S. Africa: Cape Province, Broughton nr Molteno, xii 1892, Flanagan 1632!).

P. austro-africanum (Weimar ex) R. Mill (S. Africa; Bechuanaland: Waterfalls District, 22 ii 1950, I.B. Pole Evans 77!).

Pollen oblong, ± dumb-bell shaped, equatorial constriction weak or very weak (C = 100-92). Amb hexagonal, convex, obtuse, appearing ± peritreme. P = 8-12 μm, E = 4-7 μm, B = 5-7.5 μm, D = 5.5-8 μm. P/E = c. 1.60-1.80, P/B = 1.45-1.70 (prolate). Colpi rhombic, narrowly rhombic or ± linear, bordered by bacula and furrow or by bacula only. Endoaperture a lalongate endocolpus or a nearly circular endoporus. Pseudocolpi narrower than colpi, bordered by bacula or by bacula and furrow. Collar present (usually incomplete) or absent.

1. Equatorial collar entirely absent
  2. P = 8.5-10 μm, E = 4.5-5.5 (-6) μm ..... densefoliatum
  2. P = 10.5-12 μm, E = 6-7 μm ..... austro-africanum
1. Equatorial collar present but often incomplete
  3. Equatorial collar vestigial, protruding from colpi but not from pseudocolpi ..... basuticum
  3. Equatorial collar complete or almost so, protruding from both colpi and pseudocolpi
    4. Equatorial constriction weak but perceptible (C = 92), pollen distinctly dumb-bell shaped; equatorial collar almost complete but not linking colpi with pseudocolpi ..... afrocaeruleum
    4. Equatorial constriction imperceptible (C = greater than 99), pollen practically oblong; equatorial collar complete, linking colpi with pseudocolpi ..... geometricum

4. 'suavolens' - type

Species included and material examined:

P. suavolens (R. Br.) R. Mill (Australia: Victoria, Ferntree Gully, 18 xi 1893, Morrison !).

Pollen oblong, dumb-bell shaped, equatorial constriction weak (C = 92); amb hexagonal, convex, obtuse. P = 13.5-15 µm, E = 8-9 µm, B = 9-10 µm, D = 10-11 µm. P/E = c. 1.70, P/B = c. 1.55 (prolate). Colpi rhombic, bordered by bacula and furrow. Endoaperture a lalongate endocolpus. Pseudoapertures ± rhombic. Sexine smooth.

5. '*australe*' - type

Species included and material examined:

P. australe (R. Br.) R. Mill (Australia: S. Aust., Southern mt. Lofty range c. 5 km S. of Finniss, 3 iv 1963, *Jackson* 478!).

P. drummondii (Bentham) R. Mill (S. Australia: Far Northwest, Musgrave Range, foot of mt. Harriet, 5 ix 1963, *Whibley* 930!).

Pollen oblong or dumb-bell shaped, equatorial constriction absent or weak (C = 100-92). Amb hexagonal, convex, obtuse. P = 9-11 µm, E = 5-8 µm, B = 5.5-8 µm, D = 5.5-9 µm. P/E = 1.37-1.77, P/B when constricted = c. 1.65 (pollen prolate). Colpi indistinct, narrowly rhombic, bordered by shallow furrow. Endoaperture a lalongate endocolpus. Pseudocolpi linear. Collar absent. Sexine columellate, appearing granular. Apparently binucleate.

1. Pollen oblong, ± without constriction; E = 7-8 µm ..... *australe*aust

1. Pollen dumb-bell shaped, with distinct constriction;

E = 5-6 µm ..... *drummondii*

6. '*divaricatum*' - type

Species included and material examined:

P. divaricatum (Stephan) R. Mill (China: Chark'ar nr Hsiaowutaishan, 3 vii 1931, *T.P. Wang* 503!).

Pollen dumb-bell shaped, equatorial constriction very weak (C = 96). Amb hexagonal, straight to convex, acute. P = c. 11-12 µm, E = c. 6.5-8 µm, B = c. 7-8 µm, D = 7-9 µm. P/E = 1.59, P/B = 1.53 (prolate). Colpi narrowly rhombic, bordered by bacula and furrow. Endoaperture a lalongate endocolpus. Pseudocolpi narrowly oblong. Collar absent. Sexine smooth.

7. 'amplifolium' - type

Species included and material examined:

P. amplifolium (Hochst.) R. Mill (Ethiopia: nr Zuqua'la, 2745-2950 m, 21-27 x 1926, Scott! below Goshmeda, 2745-3353 m, 22 iii 1957, Mooney 6961!).

Pollen oblong, dumb-bell shaped, equatorial constriction weak (C = 90-88). Amb hexagonal, convex, obtuse. P = 11-14 µm, E = c. 6-7 µm, B = c. 7-8 µm, D = c. 7-8.5 µm. P/E = c. 1.90-2.05, P/B = c. 1.70-1.80. Colpi rhombic. Endoaperture a lalongate endocolpus bordered by furrow. Pseudocolpi ± linear, bordered by bacula. Collar present, incomplete. Trinucleate.

8. 'javanicum' - type

Species included and material examined:

P. javanicum (Thunb.) R. Mill (Papua New Guinea: mt. Maneao, 7500 ft., 22 vi 1956, Cruttwell 754!).

Pollen dumb-bell shaped, equatorial constriction weak (C = 92). Amb hexagonal, convex, obtuse. P = c. 10.5-11.5 µm, E = c. 6.5-7.5 µm, B = c. 7-9 µm, D = c. 7-8.5 µm. P/E = c. 1.55, P/B = c. 1.40 (prolate). Colpi long, narrowly elliptic, bordered by furrow. Endoaperture a lalongate endocolpus. Pseudocolpi similar to colpi, bordered by indistinct bacula. Collar absent. Trinucleate.

9. 'glochidiatum' - type

Species included and material examined:

P. lanceolatum (Forsskål) R. Mill (Nepal: Mayangdi Khola, 2440 m, 22 iv 1954, Stainton, Sykes & Williams 2533!).

P. asperrimum (Nakai) M. Popov (Japan: Honshu, Oosaka: Takayama Higushinose-muri Toyono-sun, 400 m, 17 vi 1963, Inamasu 54!).

P. imeretinum (Kusn.) M. Popov (Caucasia, Grossheim 289!).

P. wallichii (G. Don) R. Mill (Nepal: Balle, N.W. of Bijauri, 1525 m, 26 iii 1952, Polunin, Sykes & Williams 3684!).

P. glochidiatum (Wallich) R. Mill (Afghanistan: Parvan, Panjshir valley, Jistha, 2750 m, Hedge & Wendelbo W. 5516!).

P. meeboldii (Brand) R. Mill (Bhutan: Rydak valley, Tiwpe, 1220 m, 4 vii 1914, R.E. Cooper 1173!).

P. zeylanicum (Vahl) R. Mill (Nepal: Arun valley, Lamobagar Gola, N. of Num, 1525 m, 27 v 1956, Stainton 464!).

P. amabile (Stapf & Drumm.) R. Mill (Nepal: Rabrong, Lamjung Himal, 2435 m, 27 x 1954, Stainton, Sykes & Williams 8808!).

P. paniculatum (Poepp.) R. Mill (Chile: Stock 35!).

Pollen dumb-bell shaped, equatorial constriction weak to moderate (C = 93-86). P = c. 7-11 µm, E = c. 2.5-6 µm, B = c. 3.5-6 µm, D = c. 3.5-6.3 µm. P/E = 1.80-2.20, P/B = 1.65-1.95 (prolate). Colpi linear, bordered by furrow only. Endoaperture an endocolpus or endoporus. Pseudocolpi linear. Collar absent. Sexine smooth, rarely verruculate. Trinucleate.

1. Pollen 7-8.5 x 2.5-4 µm ..... wallichii, glochidiatum & meeboldii

1. Pollen 8.5-11 x 4-6 µm

2. P/E = c. 1.80 ..... lanceolatum

2. P/E = c. 1.90-2.05

3. Equatorial constriction very weak to weak (C = 95-90)

4. P = 8-9.5 µm, E = 4-5 µm ..... asperrimum

4. P = 9.5-10.5 µm, E = 4.5-6 µm ..... imeretinum

3. Equatorial constriction weak to moderate (C = 90-85)

5. Sexine finely verruculate ..... zeylanicum

5. Sexine ± smooth

6. P = 8.7-10 µm ..... amabile

6. P = 7.9-8.7 µm ..... paniculatum

10. 'nervosum' - type

Species included and material examined:

P. nervosum (Bentham) R. Mill (India: Punjab, at mt. Dainkund nr Dalhousie,

viii 1879, J.R. Drummond 1355! Lahul: Koksar, 3660 m, 2 vi 1941, N.L. Bor 14544!).

P. stewartii (Kazmi) R. Mill (Pakistan: Hazara, Kaghan valley, Naran, 2380 m, 24 vi 1958, Burtt 877!).

P. microglochin (Bentham) R. Mill (India: Katatop Forest, Chamta State, 16 viii 1895, Lace 789!).

Similar to 'glochidiatum' - type but equatorial constriction moderate to very strong (C = 84-70). P = 7-10 µm, E = 3-4.5 µm, B = 3.5-5.5 µm, D = 3.5-5.5 µm. P/E = 2.15-2.30, P/B = c. 1.75-1.95 (prolate).

1. Equatorial constriction strong or very strong (C = 79-71) ..... nervosum

1. Equatorial constriction moderate (C = 85-80)

2. P/B = c. 1.75 ..... stewartii

2. P/B = c. 1.90 ..... microglochin

11. 'rochelia' - type

Species included and material examined:

P. rochelia (A. DC.) R. Mill (Central Madagascar, Baron 974! ibid., Ost-Imerina, Andrangoloaka, xi 1880, Hildebrandt 3644a!).

P. monophlebium (Baker) R. Mill (Central Madagascar, Baron 3307!).

P. borbonicum (Lam.) R. Mill (Balfour s.n.!).

P. cernuum (Baker) R. Mill (Central Madagascar, Baker 2033!).

P. discolor (Baker) R. Mill (Central Madagascar, x 1892, Baron 1828!).

Pollen dumb-bell shaped, equatorial constriction weak to strong (C = 93-80). Amb hexagonal, straight to convex, acute or rarely obtuse, usually ± peritreme. P = 7.0-7.8 µm, E = 3.5-5.7 µm, B = 4.2-5.9 µm, D = 3.8-5.7 µm. P/E = 1.88-2.05, P/B = 1.63-1.77 (prolate). Colpi ± linear, bordered by furrow and bacula. Endoaperture small, lalongate but practically circular. Pseudocolpi similar to colpi. Collar absent, rarely incomplete and vestigial in P. rochelia. Trinucleate.

1. Equatorial constriction strong (C = 80) ..... borbonicum

1. Equatorial constriction weak to moderate (C = 93-84)

..... cernuum, discolor, monophlebium, rochelia

The pollen of these four species is almost impossible to distinguish.

12. 'trianaeum' - type

Species included and material examined:

P. trianaeum (Wedd.) R. Mill (Colombia: Department of Canea, nr Pasto, 3050 m, 1895, R.B. White!).

Pollen dumb-bell shaped, equatorial constriction weak (C = 92). Amb 6-sided, sides alternately long and short, appearing trigonal, acute. P = c. 12.5-15 µm, E = c. 7-8.5 µm, B = c. 7.5-9 µm, D = c. 8.5-10 µm. P/E = c. 1.70- 1.75, P/B = c. 1.60. Colpi narrowly rhombic to linear. Endoaperture a small endoporus. Pseudocolpi linear. Collar absent.

13. 'limense' - type

Species included and material examined:

P. limense (Willd.) R. Mill (Chile, Rec. Ph. Germain s.n.!).

Pollen dumb-bell shaped, equatorial constriction very strong (C = 75). Amb ± peritreme, 6-sided, sides alternately long and short, convex, obtuse. P = c. 8.5-11 µm, E = c. 3.5-4.5 µm, B = c. 5-6 µm, D = c. 5.5-6.5 µm. P/E = c. 2.30, P/B = c. 1.75. Colpi narrowly rhombic, bordered by minute bacula and furrow. Endoaperture an indistinct endoporus. Pseudocolpi linear, abruptly broadening at equator into small circle. Collar absent. Sexine smooth.

20.4.2 Discussion:

All endemic African taxa have elliptic to dumb-bell shaped pollen which is apparently binucleate. Paralleling its morphological variation, P. hispidum shows considerable variation in its pollen characters, unlike most species of Cynoglosseae in which intraspecific palynological variation is small and mainly confined to quantitative characters. The collar in

Table 20.1

Quantitative Palynological Characters of Paracynoglossum

Species	C	P μm	E μm	B μm	D μm	P/E	P/B
hispidum	-	13.1 (11.2-14.6)	9.7 (8.4-10.6)	-	10.6 (9.4-11.3)	1.39	-
aequinoctiale	-	9.8 (9.2-10.4)	7.0 (6.4-7.0)	-	7.8 (7.4-8.4)	1.40	-
afrocaeruleum	92	9.2 (8.7-10.2)	5.7 (5.6-6.4)	6.2 (5.3-6.3)	6.6 (5.9-7.6)	1.61	1.48
densefoliatum	93	9.0 (8.4-9.8)	5.2 (4.6-5.6)	5.6 (5.2-6.0)	6.4 (5.6-7.3)	1.73	1.61
geometricum	99+	10.2 (9.9-10.5)	5.7 (5.6-6.4)	-	7.3 (6.9-7.7)	1.62	-
basuticum	95	9.2 (8.5-9.9)	5.6 (5.2-5.7)	5.9 (5.6-6.2)	6.2 (5.6-6.7)	1.64	1.56
austro-africanum	94	11.3 (10.5-12.0)	6.4 (6.0-7.0)	6.8 (6.0-7.4)	6.9 (6.0-7.0)	1.77	1.66
suavolens	92	14.3 (13.5-14.8)	8.5 (8.4-9.1)	9.2 (8.8-10.1)	10.8 (10.1-11.5)	1.68	1.55
australe	99+	9.7 (9.1-10.2)	7.1 (7.0-7.7)	7.1 (7.0-7.7)	8.1 (7.3-8.7)	1.37	-
drummondii	92	10.1 (9.4-11.2)	5.7 (4.9-6.0)	6.2 (5.6-6.3)	6.4 (5.6-7.3)	1.77	1.63
divaricatum	96	11.3 (10.9-11.8)	7.1 (6.6-7.7)	7.4 (7.0-8.1)	8.3 (7.3-9.0)	1.59	1.53
amplifolium	89	12.8 (11.1-13.6)	6.5 (5.9-7.1)	7.3 (7.0-7.7)	7.8 (7.1-8.4)	1.97	1.76
javanicum	92	10.8 (10.4-11.3)	7.0 (6.4-7.4)	7.6 (7.0-8.7)	7.8 (7.1-8.5)	1.54	1.42
lanceolatum	91	9.1 (8.5-9.8)	5.0 (4.5-5.5)	5.5 (4.9-5.9)	5.3 (4.6-6.3)	1.82	1.65
asperrimum	92	8.8 (8.3-9.5)	4.5 (4.1-4.9)	4.9 (4.5-5.2)	4.9 (4.6-5.0)	1.96	1.79
imeretinum	93	10.2 (9.8-10.5)	5.3 (4.6-5.9)	5.7 (5.2-6.2)	5.9 (5.5-6.4)	1.92	1.79
wallichii	91	7.3 (7.0-8.1)	3.5 (3.2-4.1)	3.8 (3.5-4.2)	4.3 (4.1-5.0)	2.08	1.92
glochidiatum	88	7.7 (7.0-8.4)	3.6 (3.1-4.1)	4.1 (3.4-4.9)	4.3 (3.8-4.8)	2.13	1.88
meeboldii	90	7.6 (6.9-8.4)	3.5 (2.8-4.2)	3.9 (3.5-4.6)	4.5 (4.2-4.9)	2.17	1.95

Table 20.1 (contd.)

Species	C	P μm	E μm	B μm	D μm	P/E	P/B
zeylanicum	86	8.8 (8.4-9.2)	4.3 (4.2-4.8)	5.0 (4.8-5.6)	4.6 (4.2-5.0)	2.04	1.76
amabile	88	9.1 (8.7-9.9)	4.5 (4.1-4.9)	4.9 (4.8-5.2)	5.2 (4.9-5.7)	2.02	1.80
paniculatum	88	8.4 (7.9-8.7)	4.2 (3.8-4.7)	4.8 (4.2-5.6)	4.9 (4.6-5.2)	2.00	1.75
nervosum	75	8.5 (7.7-9.8)	3.7 (3.1-4.2)	4.4 (3.6-4.9)	4.5 (3.6-5.0)	2.30	1.96
stewartii	82	8.8 (8.4-9.2)	4.1 (3.8-4.3)	5.0 (4.8-5.3)	4.8 (4.5-5.0)	2.14	1.76
microglochin	84	9.4 (8.7-10.2)	4.1 (3.5-4.6)	4.9 (4.5-5.0)	5.1 (4.9-5.3)	2.29	1.92
rochelia	90	8.6 (7.0-9.8)	4.5 (3.5-5.7)	5.0 (4.3-5.9)	4.2 (3.8-5.7)	1.92	1.72
monophlebium	84	7.8 (7.1-8.5)	4.0 (3.6-4.2)	4.8 (4.5-5.2)	4.7 (4.3-5.2)	1.95	1.63
borbonicum	80	7.8 (7.4-8.4)	3.8 (3.5-4.1)	4.8 (4.2-5.6)	4.5 (4.0-5.5)	2.05	1.63
cernuum	87	8.1 (7.7-8.4)	4.1 (3.5-4.6)	4.7 (4.3-4.9)	4.8 (4.5-5.0)	1.98	1.72
discolor	89	8.5 (8.0-8.8)	4.3 (3.8-4.6)	4.8 (4.6-5.0)	4.8 (4.6-5.0)	1.98	1.77
trianaeum	92	13.3 (12.7-14.7)	7.7 (7.0-8.4)	8.3 (7.7-8.7)	9.0 (8.4-9.9)	1.73	1.60
limense	75	9.9 (8.7-10.6)	4.2 (3.8-4.6)	5.7 (5.2-6.0)	6.0 (5.7-6.6)	2.31	1.74

C = index of constriction
P = length of polar axis
E = equatorial breadth
B = maximum breadth
D = polar diameter
P/E = Erdtman's ratio

P. hispidum is vestigial or absent altogether; the endocolpus, usually smooth, rarely has surface bacula, and the grains may be subprolate or well within the prolate range. This unusual range of palynological variation, together with the wide range in habit and morphology, suggests that the limits of the species be subject to revision.

Pollen of the 'afrocaeruleum' type occurs in several, mainly closely related species of Ethiopia and S. Africa. P. austro-africanum is separated from these species by its larger pollen (P greater than 10.5 μm, P/E greater than 1.75). The species within the 'afrocaeruleum' group are scarcely separable palynologically since the ranges of quantitative characters overlap and the qualitative characters do not present any clear-cut differences. There is a trend from rhombic colpi and almost complete collar (P. geometricum, P. afrocaeruleum) through narrowly rhombic colpi and vestigial collar (P. basuticum) to linear colpi and absence of collar (P. densefoliatum).

P. geometricum, which has pollen of the 'afrocaeruleum' type, was included in Cynoglossum lanceolatum by BRAND (1921). He considered that the differences in nutlet morphology between the two taxa were too small to merit the recognition of P. geometricum at specific rank. He also considered P. densefoliatum to be a transitional form between C. lanceolatum subsp. lanceolatum and subsp. geometricum. The evidence from pollen does not support this view. The pollen of P. lanceolatum is distinct from that of P. geometricum. Differential palynological characters are given in Table 20.2.

The pollen of P. lanceolatum more strongly resembles the Himalayan circle of species (pollen of 'glochidiatum' type) than the African representatives. On the other hand, P. geometricum palynologically falls naturally into the African group. Contrary to Brand, most recent African floras, e.g. AGNEW (1974), maintain P. lanceolatum and P. geometricum as separate species and the palynological evidence, along with that discussed above (sect. 20.3), has led me to follow this view.

Table 20.2

Differential Palynological Characteristics of three African species of *Paracynoglossum*

Character	*P. lanceolatum*	*P. densefoliatum*	*P. geometricum*
C	91	93	99
Amb	straight, acute	convex, obtuse	straight/convex, obtuse
P	8.5-9.8 µm	8.4-9.8 µm	9.9-10.5 µm
E	4.5-5.5 µm	4.6-5.6 µm	6.0-7.0 µm
B	4.9-5.9 µm	5.2-6.0 µm	-
D	4.6-6.3 µm	5.6-7.3 µm	6.9-7.7 µm
P/E	1.82	1.73	1.62
P/B	1.65	1.61	-
Equatorial constriction	+	+	-
Colpi	narrowly rhombic to linear	± linear	rhombic
Collar	absent	absent	present

The three Australian species are all distinct palynologically. *P. drummondii* has been treated as a variety of *P. australe* (BRAND 1921), but the marked difference in pollen morphology suggests that specific rank is more appropriate. *P. suavolens* is separated from the other two species by its larger pollen with smooth (not granular) sexine.

Palynologically, the closest relationship of *P. javanicum* seems to be with *P. australe* and especially *P. suavolens*, and shares the relatively low P/E and P/B ratios of these species. It is very distinct from the Mascarene species of sect. *Paracynoglossum*, having pollen of the '*rochelia*' type, differing from these not only by the lower P/E ratio but also in the absence of bacula bordering the colpi.

Pollen morphology has helped to establish the true relationship of P. divaricatum. This species was placed in Cynoglossum sect. Eu-Cynoglossum by BRAND (1921) and in C. subgen. Cynoglossum sect. Foliata by RIEDL (1962). POPOV (1953) also included the species in Cynoglossum, rather than in Paracynoglossum. Although he said its affinities were with C. officinale, he also pointed out that there were many sharp morphological differences, not least of which is the bracteate inflorescence. Pollen morphology suggests that the closest affinities of the species are not with Cynoglossum as here delimited, but with Paracynoglossum. If it were included in Cynoglossum it would be not only the only species to have both a bracteate inflorescence and corollas less than 5 mm, but also the only species with dumb-bell shaped pollen. As this combination of characters is more consistent with a classification in Paracynoglossum, I have transferred the species here.

Pollen of the 'glochidiatum' type is found in several Himalayan species of sect. Paracynoglossum. Palynologically the group is very homogeneous, in harmony with the close morphological relationships. Two subgroups can be distinguished on size (see key). The pollen of P. wallichii, P. glochidiatum and P. meeboldii is very similar and is evidence in support of the very close relationship between these species (KAZMI, 1971, reduced P. glochidiatum to varietal rank within P. wallichii).

P. amabile was included by BRAND (1921) in Cynoglossum sect. Eu-Cynoglossum close to C. zeylanicum and C. javanicum (both here included in Paracynoglossum). RIEDL (1962), however, removed it to subgen. Papilligerum and related it to C. viridiflorum and C. triste. Palynological evidence supports the affinity with P. zeylanicum but the pollen is unlike that of P. javanicum. The pollen is also quite different to that of either C. viridiflorum or C. triste (= Eleutherostylum triste in the present treatment). The pollen morphology supports the view proposed above (sect. 15.1) that Riedl's classification was wrong.

Pollen of the 'nervosum' type is confined to sect. Latifolia. The close relationships between P. nervosum, P. stewartii and P. microglochin were discussed by KAZMI (1971) and are substantiated by the palynological data. P. microglochin and P. stewartii are particularly close palynologically, P. nervosum differing by its stronger equatorial constriction. RIEDL (1962) placed P. nervosum in Cynoglossum subgen. Eleutherostylum while classifying P. microglochin in subgen. Paracynoglossum. Palynologically, P. nervosum is totally different to any species of the genus Eleutherostylum as here delimited, and in no way different to Paracynoglossum.

All five species from the Mascarene Islands have very similar pollen of the 'rochelia' type. Their classification has up till now been in some doubt. P. rochelia and P. monophlebium were included by RIEDL (1962) in Cynoglossum subgen. Paracynoglossum, while he placed P. borbonicum in C. subgen. Eleutherostylum. P. cernuum and P. discolor were considered imperfectly known. The many shared palynological characters strengthen my view (sects. 15.1, 20.3.3) that all five should be classified in Paracynoglossum, where they form a natural group on morphological, palynological and phytogeographical grounds. P. rochelia would appear to be the least advanced in the group palynologically since in some material a vestigial equatorial collar is present and the colpi are less narrow than in the others. P. discolor seems to be the most closely allied to P. rochelia and is also related to P. cernuum. P. monophlebium and P. borbonicum share a stronger equatorial constriction; this, together with their fractionally smaller pollen, suggests that these are the most advanced species in the group palynologically.

P. trianaeum shares with P. paniculatum the characters of pollen with weak equatorial constriction and six-sided amb, the sides of which are alternately long and short. The combination of anisolateral amb and dumbbell shaped pollen appears to be relatively common in S. American Boraginoideae, although data are limited. MARTICORENA (1968) records it in several

species, including Pectocarya boliviana, Plagiobothrys tinctorius and Nesocaryum stylosum, all members of the tribe Eritrichieae, while it is developed to an extreme in Selkirkia berteroi, where the equatorial amb view is unequally straight-hexagonal but the polar amb is ± circular. Since the pollen of P. trianaeum is 1.5-1.7 x as large as that of P. paniculatum, with narrowly rhombic (not linear) colpi which are bordered by bacula and furrow, and has lower P/E and P/B ratios, I consider that that of P. trianaeum should be recognised as a distinct pollen type. (P. paniculatum is included in the 'glochidiatum' group).

BRAND (1921) and RIEDL (1962) both considered these two species to be closely related within Cynoglossum sect./subgen. Eleutherostylum. Although I have found anisolateral ambs in some grains of Eleutherostylum virginianum, that species, in common with all species of Eleutherostylum as here delimited apart from E. triste, has oblong pollen not constricted at the equator. All the species of Eleutherostylum as here delimited are also morphologically very different and geographically isolated from both P. trianaeum and P. paniculatum.

Superficially, the pollen of P. limense resembles that of some of the Asian members of sect. Paracynoglossum, e.g. P. borbonicum. However, it is sufficiently distinct to be treated as a separate pollen type, differing by the following characters:

1. The equatorial constriction (C = 75) is one of the strongest in the genus, and the P/E ratio is equalled or exceeded only by P. nervosum of sect. Latifolia.
2. The linear pseudocolpi abruptly broaden at the equator into a minute rhombus or circle. This is apparently a rather primitive character within the genus.

20.5 CYTOLOGY

Of the 42 species of Paracynoglossum, only 10 appear to have been studied cytologically. Apart from a count for P. amabile by ZHUKOVA (1967), several by VASUDEVAN (1975) and a very recent report for P. geometricum by HEDBERG & HEDBERG (1977), all the work was done by BRITTON (1951) or earlier authors. The results are brought together in Table 20.3. Where originally published as gametic numbers, the counts have been converted here to the diploid form.

Table 20.3

Chromosome Numbers in the genus Paracynoglossum

Species	2n	Nature of source	Provenance	Reference
amabile	24	C	J.E. White, Costa Rica	Britton 1951
"	24	C	Leningrad Arctic-Alpine Botanical Garden	Zhukova 1967
"	24	W	Covindghat, Pakistan	Vasudevan 1975
lanceolatum	24	W	Banihal, Kashmir	Vasudevan 1975
glochidiatum	24	C	Hort. Hauniensis, Copenhagen, Denmark	Britton 1951
"	24	C	Uppsala, Sweden	Britton 1951
wallichii	24	C	G. Ghose & Son, Darjeeling, India	Britton 1951
"	24	W	Nainital, W. Himalayas	Vasudevan 1975
zeylanicum	24	C	Pearce Seeds, New Jersey, U.S.A.	Britton 1951
"	24	W	Qurez, Kashmir	Vasudevan 1975
"	24	W	Nainital, W. Himalayas	Vasudevan 1975
aequinoctiale	48	C	Hort. Bot. Bergianus, Stockholm, Sweden	Britton 1951
geometricum	24	W	Cameroon Mountain	Hedberg & Hedberg 1977
petiolatum	24	W	Gulmarg, Kashmir	Vasudevan 1975
nervosum	24	C	?	Sugiura 1940
"	24	C	Pearce Seeds, New Jersey, U.S.A.	Britton 1951
"	24	W	Almora, Pakistan	Vasudevan 1975
microglochin	24	W	Nainital, W. Himalayas	Vasudevan 1975

W = material of known wild origin C = cultivated material

With one exception, all the species are diploid with $2n = 24$, the most widespread number in the Cynoglosseae. P. aequinoctiale was stated to have $2n = 48$ and thus is the only known polyploid, assuming that the identification by the Stockholm garden was correct.

The chromosomes are very small, consistently smaller than those of Cynoglossum. Those of P. wallichii are particularly small. This size difference, if maintained when a larger range of species is studied, would be a useful micro-character to support the separation of Paracynoglossum from Cynoglossum proposed on the basis of macromorphology.

All species have a preponderance of acrocentric or telocentric chromosomes, with few metacentric ones. This advanced character correlates well with the advanced nature of many of the gross morphological features (e.g. small self-fertilised flowers, small nutlets) and pollen characters (e.g. dumb-bell shape).

20.6 CHEMOTAXONOMY

In contrast to Cynoglossum, Paracynoglossum has received little attention from chemotaxonomists. Four pyrrolizidine alkaloids have been reported:

amabiline ($C_{15}H_{25}NO_4$): recorded from P. amabile by CULVENOR & SMITH (1967) and by MAN'KO (1972).

cynaustraline ($C_{15}H_{27}NO_4$): } both recorded from P. australe (CULVENOR & SMITH 1967)
cynaustine ($C_{15}H_{25}NO_4$): }

echinatine : recorded from P. amabile by JERMANOWSKA & SYKULSKA (1967) and by MAN'KO (1972).

Apart from the widespread alkaloid echinatine, none of the Cynoglossum alkaloids have been discovered in Paracynoglossum, and the three alkaloids amabiline, cynaustraline and cynaustine have not been recorded outside Paracynoglossum. Much more work is needed, but the limited data provide evidence of a lack of chemical relationship between Cynoglossum and Paracynoglossum. If the pattern is maintained when further species are analysed,

it will provide additional evidence for the recognition of Cynoglossum and Paracynoglossum as separate genera.

20.7 RELATIONSHIPS

20.7.1 Intrageneric:

Relationships within Paracynoglossum are less reticulate than in the other large genus of Cynoglosseae, Paracaryum. The four sections recognised here are quite clear-cut, although sects. Latifolia and Paracynoglossum are connected by P. microglochin. Sect. Limenses is very distinct palynologically and morphologically. Its species require further collection and study so that its relationships with the rest of the Cynoglosseae can be properly understood. At present I have included it in Paracynoglossum but the differences are such that it might need higher status. It seems to be connected to Paracynoglossum by P. paniculatum, whose relationship within Paracynoglossum is itself obscure. I have included it in sect. Paracynoglossum as it is similar to the P. amabile group in leaf and floral characters. However, it differs by its much larger nutlet attachment scar and by its pollen with anisolateral amb, a character shared only by its S. American congeners P. trianaeum and P. limense.

Within sect. Paracynoglossum, I have recognised several informal groups on the basis of leaf morphology (see sect. 20.3.3). Species within these groups frequently also share common floral, nutlet and pollen characters, and the groups undoubtedly represent natural circles of affinity. As there are few discontinuities between groups, however, but rather a continuous range of variation, it has not proved possible to construct a workable key which would allow them to be given formal series or subsectional rank.

20.7.2 Intergeneric:

Paracynoglossum is most clearly related to Ivanjohnstonia and Cynoglossum. From Ivanjohnstonia it is separated by the regular calyx which accresces in fruit by not more than 150%, rather than by 700% as in Ivanjohnstonia.

Relations with Cynoglossum are close but the genus is distinguished by the nutlets free from the style. Most species are also palynologically distinct, having dumb-bell shaped (not elliptic) pollen. Several African species, e.g. P. hispidum and P. aequinoctiale, do have elliptic unconstricted pollen, however, and these connect the genus with Cynoglossum. P. hispidum is also similar to some species of Cynoglossum in its dull red corollas, rather than the blue colour so predominant in Paracynoglossum, but known in Cynoglossum only in C. tianschanicum, C. pringlei and C. henricksonii.

CHAPTER 21

13. IVANJOHNSTONIA Kazmi

21.1 INTRODUCTION

This monotypic Himalayan genus was first described by KAZMI (1975), based on a specimen from Jaunsar collected by Gamble in 1898 and referred by him to Cynoglossum. The genus is known only from the holotype at Kew, which is of a mainly fruiting plant and is in a rather poor state of preservation; however, Riedl (personal communication) has informed me that there is a sheet at Vienna Museum (W) which may belong to Ivanjohnstonia. Kazmi related the genus to Cynoglossum, distinguishing it by its unequal calyx lobes much larger in fruit, the pyramidal-subglobose gynobase, and the suberect nutlets with larger attachment scar.

21.2 SYSTEMATIC TREATMENT

Ivanjohnstonia Kazmi in Sultania 1:1 (1975).

Type: I. jaunsariensis Kazmi, loc. cit. (1975).

Perennial herb. Rootstock unknown. Stem erect, hollow, finely striate, rather stout (to 1 cm diam.), branched, with moderately dense indumentum of short, retrorsely adpressed or subadpressed trichomes 0.4-0.7 (-1) mm, not arising from tuberculate bases. Basal leaves unknown. Cauline leaves alternate (uppermost subopposite), shortly petiolate to subsessile; lamina broadly oblong-ovate to broadly lanceolate, thin and membranous, very brittle when dry, obtuse, entire, median 110-120 x 30-35mm, ± attenuate at base; midrib prominent but not elevated, principal veins c. 7, indistinct, their surface rather densely covered with 0.1-0.3 mm hyaline trichomes, antrorsely adpressed above, retrorsely adpressed beneath, arising from minute bulbous bases. Inflorescence a branched terminal panicle of scorpioid cymes, elongating at maturity to 75 cm; flowers ± remote, internodes lengthening further in fruit. Cymes bracteate, bracts

leaf-like, to 5 x 2.5 mm in flower, enlarging to 40 x 25 mm in fruit and then caducous. Pedicels slender, decurrent on to inflorescence axis, 1-7 mm at anthesis, thickening and elongating in fruit to 15-20(-35) mm in length. Calyx divided to base, lobes 5, unequal, ovate to lanceolate, acute, 3.5-4 x 1.8-2.5 mm in flower, greatly accrescent in fruit and reaching 25 x 15 mm, densely covered on outer surface with antrorsely adpressed 0.1 mm setules, sparsely hairy on outer surface, with much longer 0.5 mm setules on margin and at apex. Corolla bluish-purple, campanulate-infundibular, slightly contracted at throat, to 3 mm long, tube and limb subequal, limb divided to base, lobes oblong-ovate or ovate. Faucal scales broader than long, semi-lunar or trapeziform, slightly emarginate, c. 0.1 x 0.3 mm. Stamens included. Filaments very short (c. 0.2 mm), inserted in upper part of tube; anthers oblong-ovate, not sagittate or mucronate, their bases not or scarcely reaching base of scales. Ovary 4-lobed. Style fleshy, ± quadrangular-prismatic, to 1 mm, shorter than gynobase. Style discoid. Gynobase pyramidal-subglobose, with 4 large basal pits. Nutlets greyish- or greenish-white, ovate, 2-3 x 1.5-2 mm, free from the style, attached to gynobase by ovate to suborbicular ventro-apical scar slightly smaller than nutlet; dorsal surface somewhat flattened, ± keeled; whole surface of nutlets evenly glochidiate-aculeate and minutely punctate between glochids; glochids 0.5-0.7 mm, with 3-5 apical barbs.

21.3 MORPHOLOGY AND RELATIONSHIPS

In general habit *I. jaunsariensis* resembles some species of *Paracynoglossum* but differs from all of them by the unequal calyx lobes which greatly enlarge in fruit to up to 7 times their original size (Fig. 18.1, no. 7). The calyx lobes are very slightly unequal in several genera of Cynoglosseae (e.g. *Rindera*, *Paracaryum*) but the difference in size is so slight as to be scarcely detectable. In *Ivanjohnstonia* the inequality is quite pronounced and in this respect the genus is apparently unique

in the tribe. The great enlargement of the lobes in fruit is reminiscent of Suchtelenia, Omphalodes ripleyana and to a lesser extent Asperugo (tribe Asperugeae).

The leaves of Ivanjohnstonia are similar to certain species of Paracynoglossum sect. Latifolia in their venation, but differ by their more oblong outline. The venation is markedly different to the triplinerved Himalayan species of Paracynoglossum (e.g. P. amabile, P. wallichii, P. zeylanicum) not only in vein number but also in the fact that they are not elevated beneath. The even, moderately dense indumentum, the hairs not arising from tuberculate bases is closer to that of P. sect. Latifolia than to P. sect. Paracynoglossum.

The small bluish corollas and small nutlets (Fig. 18.1, no.6) also point to a relationship with Paracynoglossum. The very small corollas are markedly different in size to those of P. sect. Latifolia and are closer to P. sect. Paracynoglossum. There are no important morphological differences by which the corollas of the two genera can be distinguished.

Kazmi emphasised the pyramidal-subglobose gynobase as a diagnostic generic character. There are certain trends towards this type of gynobase in Paracynoglossum but in Ivanjohnstonia the trend is taken to an extreme. The fact that the nutlets are free from the style was not noted by Kazmi, and is further evidence of a relationship with Paracynoglossum, as is the general nutlet morphology.

There is no relationship with Cynoglossum as recognised here, from which Ivanjohnstonia differs by the small nutlets free from the style, small corollas, etc. Nor is there any close relationship with Paracaryopsis, which differs by its very large leathery leaves which have dense tuberculate-based trichomes, and by its larger flowers.

Although it would be possible to accommodate Ivanjohnstonia within the limits of its nearest relatives, Paracynoglossum, if a broad view of generic limits were taken, it would require at least sectional rank. Its many

distinctive features suggest, however, that Kazmi's recognition at generic rank is a more appropriate treatment. The genus is characterised by a peculiar mix of relatively primitive characters (bracteate cymes, subrhombic pollen colpi) and relatively advanced ones (small, presumably self-pollinated flowers, small nutlets).

21.4 PALYNOLOGY

Material examined: N.W. Himalayas: Jaunsar, 2135 m, x 1898, J.S. Gamble 27383;

21.4.1 Description:

Pollen rather small, oblong, dumb-bell shaped, equatorial constriction weak (C = 92); heterocolpate, tricolporate, tripseudocolpate. Amb appearing ± circular, hexagonal, convex, obtuse, pseudoapertures included. P = 10.4 (9.6-11.3) μm, E = 5.5 (5.2-6.5) μm, B = 6.0 (5.6-6.9) μm, D = 6.5 (6.0-6.9) μm. P/E = 1.89, P/B = 1.73 (prolate). Colpi narrowly rhombic, bordered by bacula. Endoaperture a ± lalongate endocolpus. Pseudocolpi narrowly rhombic to ± linear, bordered by bacula. Collar absent. NPC = 345. Sexine ± smooth.

21.4.2 Discussion:

The pollen of Ivanjohnstonia closely resembles that of many species of Paracynoglossum, although the constriction is weaker than in some species, and the colpi are more distinctly rhombic. The latter is probably a primitive feature in line with certain other primitive aspects of the general morphology, such as the bracteate cymes. The slightly rhombic colpi possibly represent a transitional stage from the rhombic colpi of Cynoglossum and a few species of Paracynoglossum to the ± linear ones found in most species of Paracynoglossum(see sect. 4.8).

The pollen is unlike that of Cynoglossum as here defined, differing by its dumb-bell shape with equatorial constriction, and by the absence

of an equatorial collar in addition to the much more narrowly rhombic colpi. From the pollen of Austrocynoglossum it differs primarily by its much smaller size.

Palynological research therefore confirms the close affinity with Paracynoglossum established on the basis of gross morphology. However, there are no peculiar palynological features which characterise the genus, in contrast with its gross morphological characters.

CHAPTER 22

14. TYSONIA H. Bolus

22.1 INTRODUCTION

The genus Tysonia was first described by BOLUS (1890). As here defined it comprises three species, T. africana, T. glochidiata and T. campanulata, the latter two being described as new by the present author. The genus has a disjunct distribution in Southern and Eastern Africa: T. africana and T. glochidiata occur in Natal and the Transkei, while T. campanulata is endemic to Tanzania (Map 22.1).

The salient features of Tysonia as characterised by Bolus were its tall habit with very large basal leaves and large, many-flowered paniculate inflorescence; subrotate corolla with subpatent to reflexed lobes; versatile anthers exserted from the corolla tube on long filaments; long, exserted faucal scales; well developed nectaries at base of corolla tube; and relatively large nutlets (1 x 1.5 cm) lacking glochids but with a broad rugulose cartilaginous wing. Bolus related the genus to Caccinia, Solenanthus and Rindera, and also noted certain parallels with the New Zealand species Myosotidium hortensia.

BRAND (1921, p. 89 f. 11) included Tysonia in his treatment of the Cynoglosseae. Although in most aspects his account and illustration refer to Bolus's plant, his description of the nutlets differs considerably. These were said to be broadly ovate, c. 7 mm long, and densely glochidiate (cf. his fig.11e, f). JOHNSTON (1924b, p. 72) commented that 'the plant described and figured by Brand ... is obviously quite different from T. africana in fruiting structures, having the depressed ... densely glochidiate wingless nutlets of a Cynoglossum'. As the genus was unrepresented in the Gray Herbarium, however, he was unable to assess the status of Brand's plant. Since then, doubt has been cast by the authors of some African floras (e.g. DYER 1975), as to whether the fruit figured by Bolus

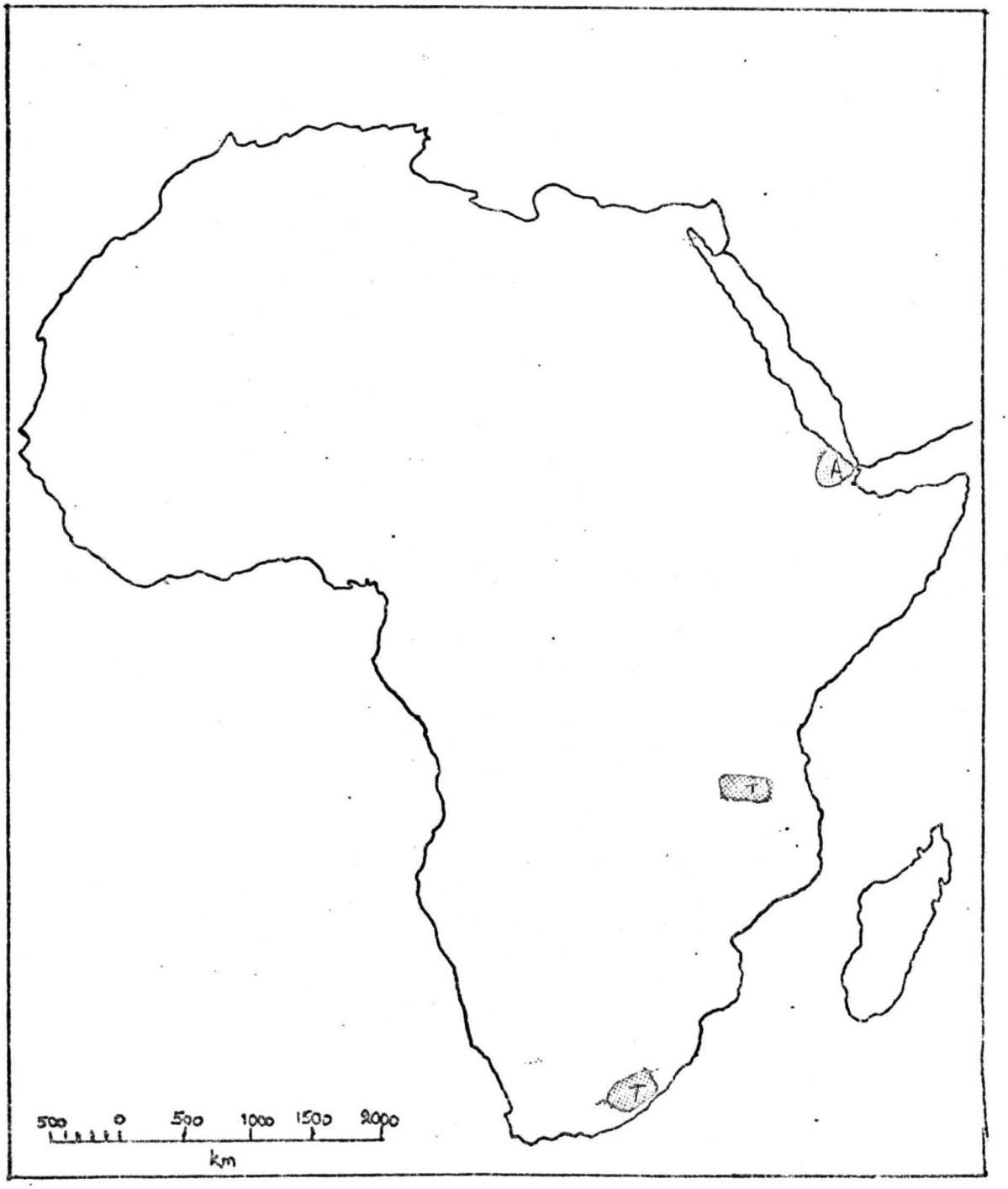
and contained in the capsule on the type sheet actually belonged to Tysonia - DYER (1975) considered it to be that of a species of Trichodesma.

I have examined several sheets of material labelled T. africana in Edinburgh and Kew herbaria, including the type specimen (Tyson 2117 from East Griqualand, now part of Transkei). Of these, one specimen at E (Wood 973) is a duplicate of one of those cited under T. africana by Brand. It closely matches the type in having very broad, somewhat truncate ovate basal leaves and relatively large flowers (7 mm long) with an 8 mm style, but lacks nutlets. All the other specimens at E, and most of those at K, differ from the type and the Wood specimen in their more elliptic basal leaves with denser, greyish, softer indumentum, and smaller flowers with shorter calyx lobes and usually shorter style. One gathering (Hilliard 5487 - E, K) bears rather immature nutlets. These are small (c. 4 x 3 mm), but lack even a rudimentary wing. Instead, they are densely glochidiate, resembling those illustrated by Brand and quite unlike the nutlet of T. africana.

The evidence so far presented suggests the existence of two distinct taxa in S. Africa, differing in nutlet morphology and other characters. In order to verify the nature of the nutlets of T. africana, Burtt (pers. comm.) visited the Transkei and Natal in the summer of January 1978. T. africana was re-discovered from two sites, one in Natal, the other in Transkei overlooking Clydesdale, the type locality. Several plants were observed and collected; most were in leaf, a few in flower and one was bearing ± ripe nutlets. Living material is now in cultivation at Edinburgh, and herbarium material is at E and NU. The nutlets are similar in morphology to those on the type sheet of T. africana, possessing a broad wing with undulate margin, and lacking glochids. The distinctness of the two taxa is thus confirmed and previous doubts as to the authenticity of the nutlets on the type sheet are dispelled. The name T. glochidiata R. Mill

Map 22,1

Distribution of Tysonia & Adelocaryum



T Tysonia

A Adelocaryum

has been proposed for the species with glochidiate nutlets and greyish, elliptic radical leaves (MILL in BURTT 1979, in press).

There is material at Kew of a third taxon belonging to Tysonia. Collected much farther north, in Tanganyika Territory (now part of Tanzania), these specimens (Richards 8679, 16809) differ from the two southern African species by their campanulate corollas with scarcely reflexed lobes, hardly exserted anthers, short style equalling the corolla but not exserted, shorter pedicels, and absence of secondary branches in the inflorescence. I consider them to represent a third species, here named T. campanulata R. Mill, which is markedly disjunct in its distribution, representing a considerable extension of the known range of the genus.

Accepted Taxa:

T. africana H. Bolus

T. campanulata R. Mill

T. glochidiata R. Mill

22.2 SYSTEMATIC TREATMENT

Tysonia H. Bolus in Hooker's Ic. Pl. 20: t. 1942 (1890).

Type: T. africana H. Bolus, loc. cit. (1890).

Erect, perennial tall herbs. Stems single from short, vertical rootstock clothed with old petiolar remnants, unbranched in vegetative part, finely striate, terete, ± glabrous below, with antrorsely or retrorsely adpressed setiform hairs above and in inflorescence. Basal leaves long-petiolate; lamina broadly ovate or elliptic, to elliptic-lanceolate, prominently veined, minutely puberulous ('scabrid' - WRIGHT in THISELTON-DYER, 1904) to strigillose. Lower cauline leaves long-petiolate, upper sessile; lamina elliptic, narrowly elliptic or narrowly lanceolate, base attenuate to cuneate, apex acute to acuminate; lower surface densely puberulous to strigillose, more sparsely strigillose above, either all

hairs lacking tuberculate bases or some arising from multicellular tubercles. Inflorescence a large, lax branched panicle, with or without secondary branches, bracteate; either all bracts reduced or lower ones leaf-like. Cymes 8-15-flowered, simple or branched, pedunculate; peduncles with 1-2 (second-order) bracts shorter than those on the inflorescence (first-order bracts). Pedicels ebracteolate, elongating considerably in fruit, with sparse, thin, antrorsely adpressed setiform hairs. Calyx divided ± to base into 5 equal, lanceolate lobes, persistent but hardly accrescent in fruit, shorter than pedicels. Corolla white (sometimes tinged mauve) to dull yellow, campanulate or subrotate, 4-9 mm; limb lobed ± to throat, lobes patent to subreflexed, 1.5-5 mm, ovate, obtuse, sometimes rather fleshy; faucal scales exserted from throat, trapeziform, oblong-triangular or semilunar, 0.6-2.5 x 1-2 mm, apex usually emarginate, with or without dense oblong marginal papillae. Filaments inserted in middle of tube well below scales, 3-6 mm, ± exserted from corolla, surpassing scales, dilated at base; anthers oblong, medifixed, versatile. Nectary scales c. 10, situated at extreme base of corolla tube, each with 2 divergent horns. Ovary on thick, semiglobose receptacle, indistinctly 4-lobed at apex; style filiform, subequalling stamens or slightly shorter; stigma small, capitate. Nutlets 1-4, attached to gynobase by apical, triangular to lanceolate scar, all equal or one much larger than others; either depressed, wingless and densely glochidiate, or larger, strongly laterally compressed, lacking glochids but with broad, cartilaginous ± undulate wing. 'Seed erect, affixed below apex of nutlet, exalbuminous, ovate, compressed; testa conspicuously veined, veins curved; cotyledons cuneate-obovate, plano-convex, much larger than the very short radicle' (BOLUS 1890).

1. Corolla campanulate; anthers scarcely exserted; faucal scales semilunar, 0.6-0.7 x 1.5-2 mm ..... 3. campanulata

1. Corolla subrotate; anthers considerably exserted; faucal scales trapeziform to oblong-triangular, 1.5-2.5 x 1-1.5 mm
   2. Nutlets 9-11 x 10-15 mm, with broad undulate marginal wing; corolla 7-9 mm; basal leaves broadly ovate, lamina 22-26 x 13.5-18 cm ..... 1. africana
   2. Nutlets (4-) 7 mm, lacking wing, densely glochidiate; corolla 4-6.5 mm; basal leaves elliptic, lamina 14.5-23 x 6.5-8 cm ..... 2. glochidiata

1. T. africana H. Bolus in Hooker's Ic. Pl. 20: t. 1942 (1890). (Fig. 22.1).

Plant 80-120 cm. Basal leaves broadly ovate, lamina 22-26 x 13.5-18 cm, base obtuse to truncate, then abruptly cuneate or attenuate into petiole; apex acuminate; lower surface densely puberulent, hairs very short, etuberculate, upper surface strigillose. First-order bracts to 50 x 6 mm, narrowly lanceolate, strigillose, arising just below distal end of peduncle or about halfway; second-order bracts similar, 10 x 1 mm. Peduncles 1-2 cm; pedicels 8-25 mm at anthesis, elongating to 35 mm in fruit. Corolla white or yellow, sometimes with mauvish tinge, 7-9 mm; tube 3-4 mm; limb 4-5 mm; filaments 5-6 mm, inserted 0.5-1 mm below scales; scales c. 2 x 1.5 mm; style c. 8 mm. Nutlets 9-11 x 10-15 mm, often solitary by abortion, subdisciform, strongly laterally compressed, with broad, rugulose, undulate, cartilaginous wing; glochids absent; disc orbicular, glabrous. Fl. 12-4. Hillsides nr streams, 915-1830 m.

Type: (S. Africa, Transkei) juxta rivulos circa Clydesdale, Griqualand Orientalis (Kaffrariae provincia), alt. c. 3000 ped., fl. Dec., W. Tyson 2117 (holo. K!). S. Africa, Transkei: Umzimkulu District, farm 'Ebuta', mt. Malowe, overlooking Clydesdale, 17 i 1978, Hilliard & Burtt 11219! Natal: Ixopo, Sutton Estate, 16 i 1978, Hilliard, Burtt & Shirley 11210! ibid., Shirley s.n. Polela, 1525-1830 m, 6 iv 1892, I. Medley Wood 973!

Figure 22.1

Tysonia africana: Morphology

1 Basal leaf, x 0.44 (Hilliard & Burtt 11219)

2 Upper surface indumentum, basal leaf, x 35 (Hilliard & Burtt 11219)

3 Lower surface indumentum, basal leaf, x 35 (Hilliard & Burtt 11219)

4 Inflorescence, x 0.45 (Tyson 2117)

5 Calyx and style, x 8.7 (Hilliard & Burtt 11210)

6 Corolla opened out, x 8.7 (Tyson 2117)

7 Nutlet, dorsal view, x 4.4 (Hilliard & Burtt 11210)

8 Nutlet, ventral view, x 4.4 (Hilliard & Burtt 11210)

Figure 22,1

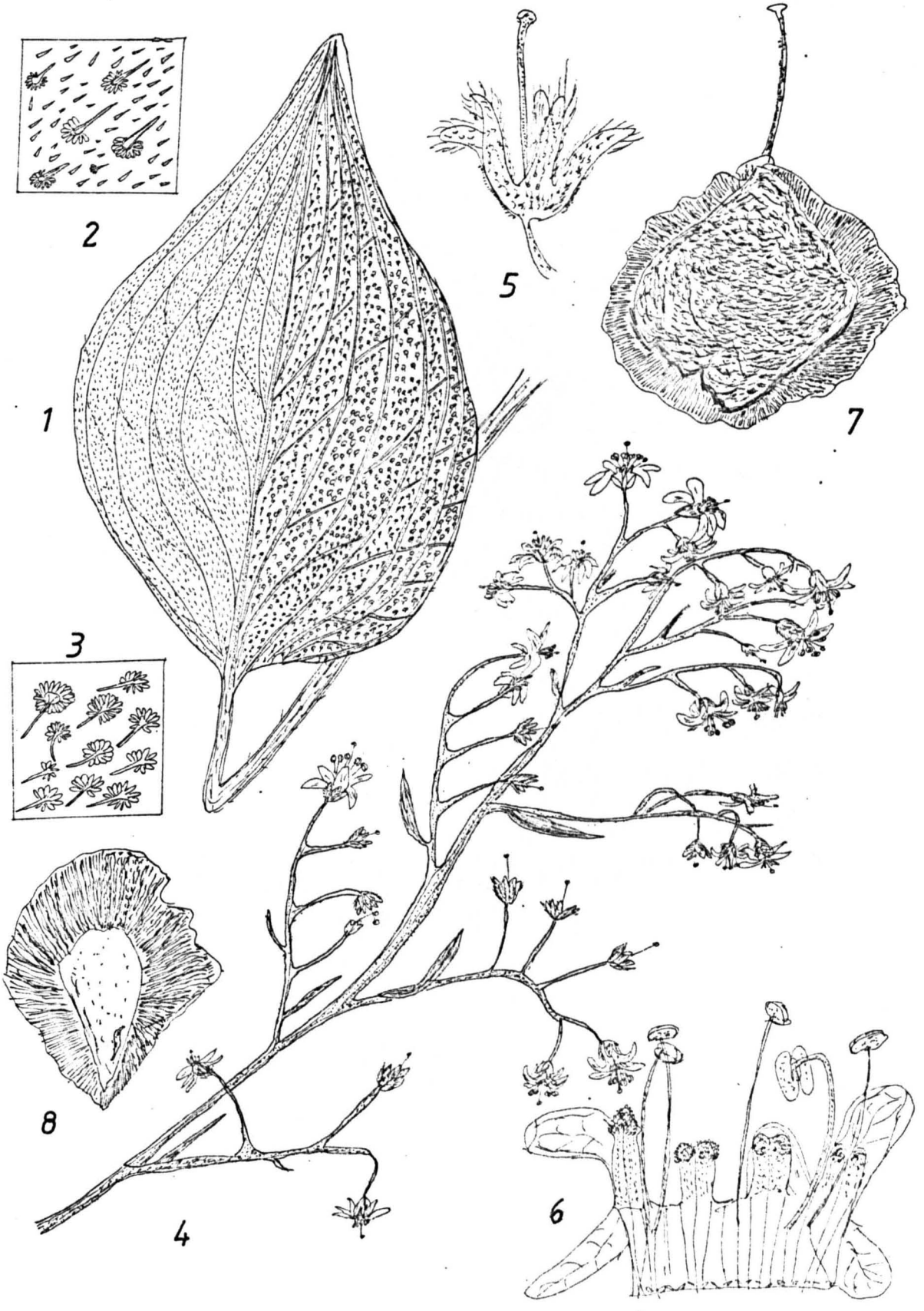


Figure 22.2

Tysonia glechidiata: Morphology

(All drawings made from the type gathering, Hilliard & Burtt 5487)

1 Basal leaf, x 0.45 (left side: upper surface; right side: lower surface)

2 Basal leaf indumentum, upper surface, x 35

3 Basal leaf indumentum, lower surface, x 35

4 Inflorescence, x 0.45

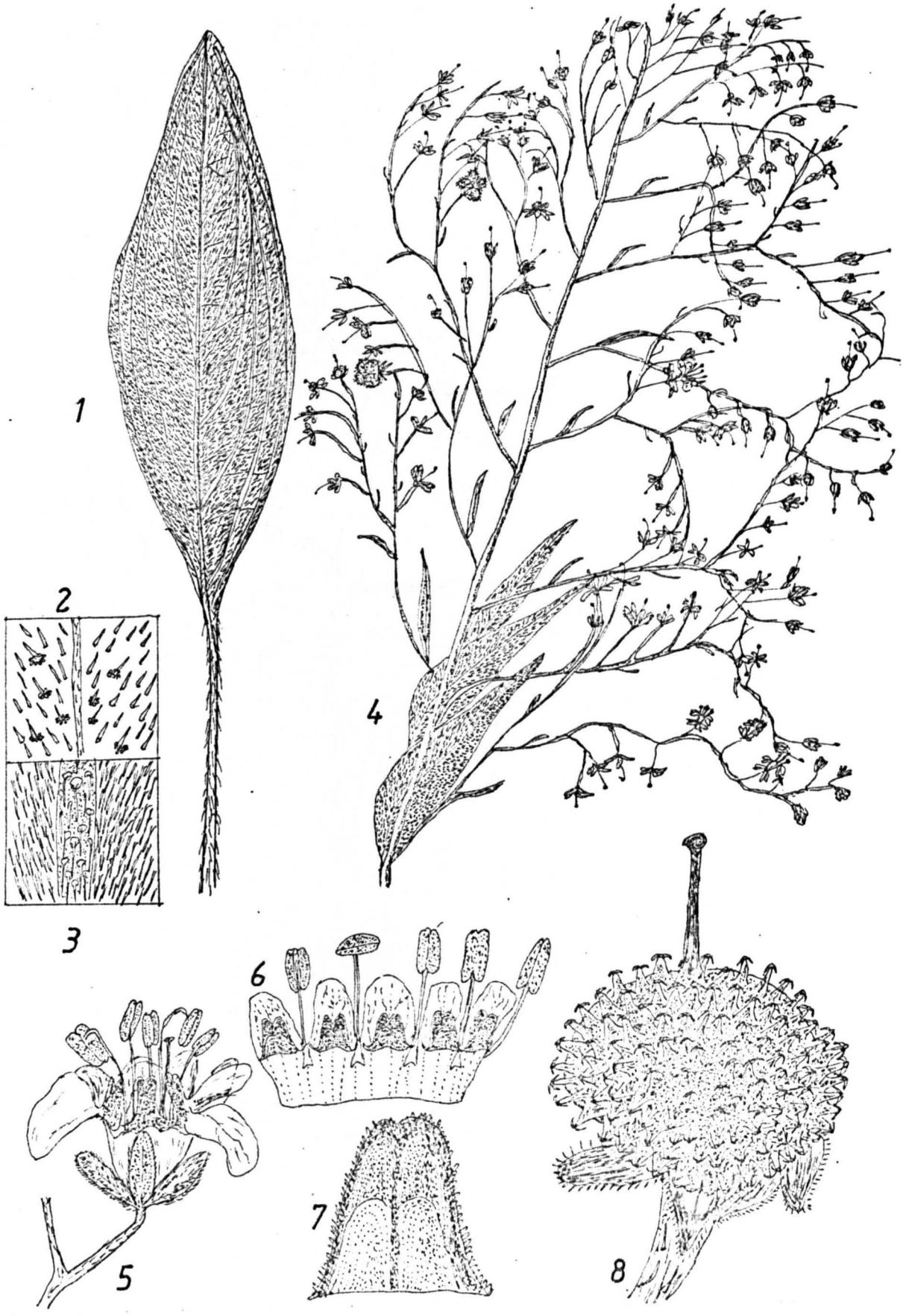
5 Corolla and calyx, x 4.4

6 Corolla opened out, x 4.4

7 Faucal scale, x 17.5

8 Nutlet and style, x 8.7

Figure 22,2



2. T. glochidiata R. Mill in Notes R.B.G. Edinb. (1979, in press).

(Fig. 22.2).

Plant 70-120 cm or more. Basal leaves elliptic, lamina 14.5-23 x 6.5-8 cm, base gradually cuneate, apex acuminate, sometimes with c. 1 mm mucro; lower surface very densely retrorsely strigillose, upper surface sparsely scabrid-setulose. Cauline leaves narrowly elliptic to narrowly lanceolate, median 10-20 x 1.3-5 cm, base attenuate, apex acuminate; upper surface antrorsely or patent-strigillose, hairs usually arising from small tubercles, larger setiform hairs (c. 1% of total) always arising from large tuberculate bases surrounded by 1(-2) rows of suborbicular subsidiary cells; lower surface densely retrorsely strigillose. First-order bracts 15-30 x 1-10 mm, strigillose, hairs arising from tuberculate bases; second-order bracts similar, smaller. Branches 5-14 cm. Peduncles 1.5-5 cm; pedicels at anthesis 5-20 mm, elongating to 15-60 mm in fruit. Corolla white, creamy or yellow, sometimes with mauvish tube, 4-6.5 mm; tube 1-3 mm, lobes 2.5-4 mm; filaments 5-6 mm, inserted 0.5-1 mm below scales; scales 1.5-2.5 x 1-1.2 mm. Nutlets c. 7 mm at maturity, 1-4, depressed-ovoid, lacking wing, densely glochidiate. Fl. 1-3. Forest margin scrub, grassveld, moist depressions and gullies, 1450-1950 m.

Type: South Africa, Natal, Alfred District, Weza, Zuurberg, 1580 m, in forest margin scrub, c. 120 cm, corolla lobes creamy, tube mauvish, but mostly in fruit, 3 iii 1974, O.M. Hilliard 5487 (holo. E! iso. E! K! NU!).
South Africa. Natal (Upper Drakensberg): Estcourt District, Giant's Castle Reserve, 13 ii 1964, M. McKeown 107! ibid., 10 ii 1964, M. McKeown 88! ibid., 3 ii 1966, W.R. Trauseld 562! foot of Drakensberg, 9 i 1886, White 3557! Cathkin Peak, 6 i 1968, Strey 7819! Cathedral Peak, Forest Research Station, 6350 ft., Killick 1360! Alpindhlu District, Vergelegen Nature Reserve, Mahlangubo river valley, Hilliard & Burtt 11158! Nahai river, Bergville, 4700 ft., 4 xii 1928, Galpin 9737!

Burtt (in litt.) cites the following additional specimens of T. glochidiata, all deposited at NU; Natal: Polela Distr., Bulwer, 1525 m, i 1931, Bayer 369. Glengarriff, 5500 ft., 5 i 1976, Rennie 718. Estcourt District, Kamberg, 6300 ft., 2 iii 1974, Wright 1727. Champagne Castle, 5400 ft., i 1942, Bayer 1255. Bergville District, National Park, 5600 ft., 3 ii 1955, Edwards 541. The Caverns, 4800 ft., i 1956, Hodson 10. Klips River District, Van Reenes, 5000 ft., 22 i 1908, Wood 10742.

3. T. campanulata R. Mill, sp. nov. (Fig. 22.3).

Young basal leaves lanceolate-elliptic or narrowly lanceolate-elliptic, lamina to 12 x 3 cm, obtuse to acute, attenuate at base into 8-10 cm petiole; upper surface deep green, with scattered long thin etuberculate hairs to 1-1.5 mm; lower surface with scattered setiform hairs, 0.8-1.5 mm, arising from multicellular tubercles. Cauline leaves numerous, lower unknown, upper ones sessile, elliptic to lanceolate-ovate, to 13 x 4 cm, acute or acuminate, cuneate at base. Inflorescence paniculate but lacking secondary branches, bracteate; at least lower bracts leaf-like, 80-100 x 25-27 mm, upper ones and second-order bracts reduced, linear-lanceolate. Peduncles 2-4 cm. Pedicels 6-9 mm at anthesis. Calyx 3.5-5 mm, greyish, with dense short hairs. Corolla white, campanulate, 7-9 mm; tube 5.5-6 mm; lobes 1.5-2 mm, broadly oblong-ovate, emarginate, rather fleshy, patent or hardly reflexed. Faucal scales semilunar or compressed-trapeziform, 0.6-0.7 x 2 mm, exserted. Filaments 3 mm, inserted in middle of tube. Anthers just exserted from corolla tube, 1.3 x 0.5 mm, yellowish. Style 4-5 mm, slightly shorter than corolla tube or sometimes just exserted, lengthening slightly after anthesis. Nutlets unknown; immature ovules (after anthesis) warty (young glochids?) and apparently wingless. Fl. 3. Very rough grassland, 2100-2400 m.

Type: (Tanzania) Tanganyika Territory, Ufipa District, Sumbawanga, Mbesi Forest, 2400 m, 13 iii 1957, in very rough grassland, H.M. Richards 8679 (holo. K!). Tanzania: Tanganyika Territory, Ufipa District, Sumbawanga, Malanji farm land, 19 vii 1962, 2100 m, H.M. Richards 16809 (basal leaves only)

Figure 22.3

Tysonia campanulata: Morphology

1 Rootstock and young basal leaves, x 0.2 (Richards 16809)

2 Young basal leaf, x 0.87 (Richards 16809)

3 Basal leaf indumentum, upper surface, x 35 (Richards 16809)

3a trichome, x c. 85

4 Basal leaf indumentum, lower surface, x 35 (Richards 16809)

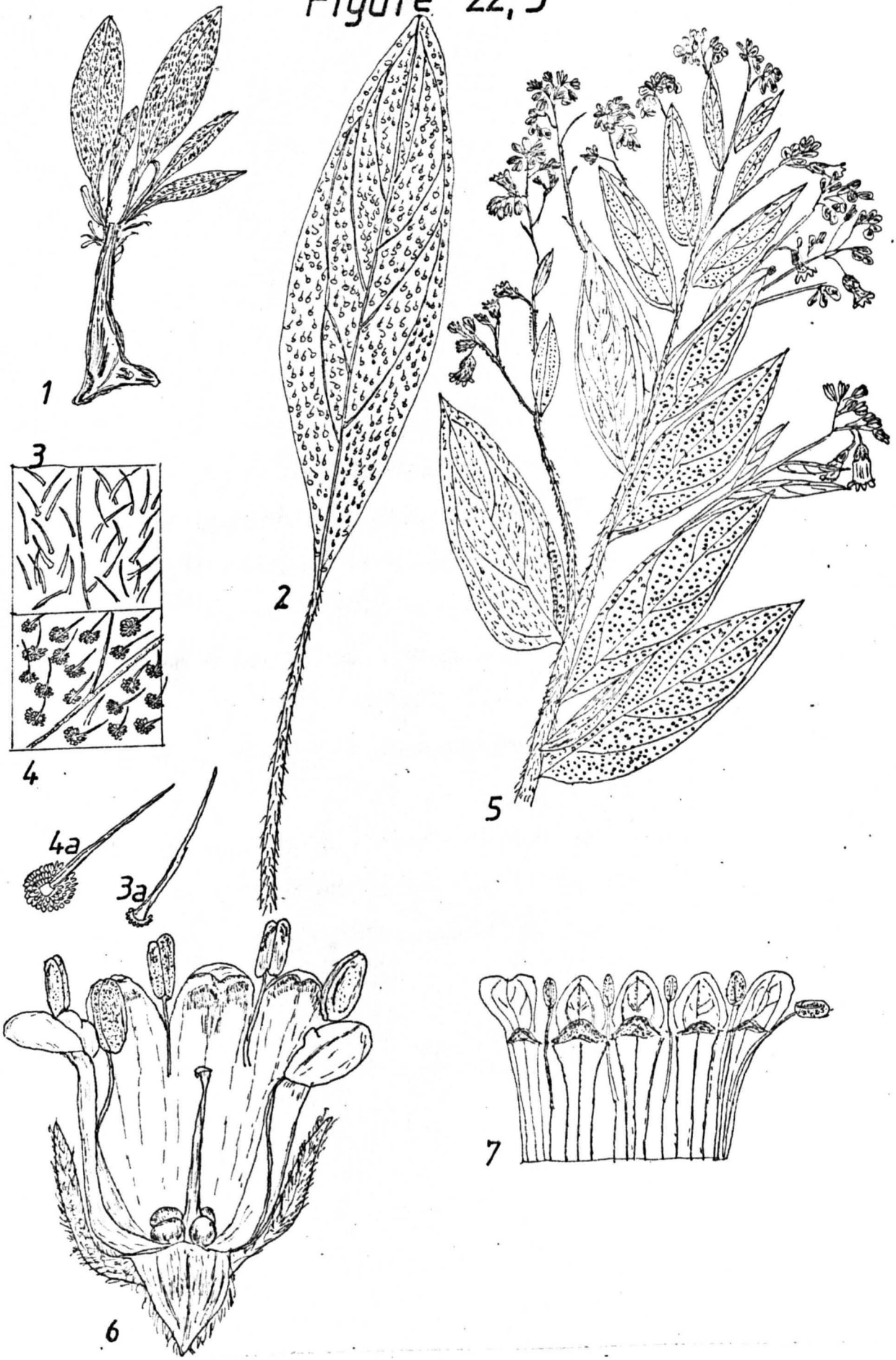
4a trichome, x c. 85

5 Inflorescence and upper cauline leaves, x 0.45 (Richards 8679)

6 Corolla, calyx and gynoecium, x 8.7 (Richards 8679)

7 Corolla opened out, x 4.4 (Richards 8679)

Figure 22, 3



22.3 MORPHOLOGY

The three species of Tysonia are perennial tall herbs of the veld, often occurring near streams and at the margins of forests.

22.3.1 Rootstock:

The rootstock appears to have been rarely collected; those I have seen are short, fusiform and vertical, clothed with old petiolar remnants, and are similar to but not as strongly developed as the rootstock in Solenanthus, Rindera and allied genera.

22.3.2 Leaves:

The very large, long-petiolate basal leaves are a distinctive feature of Tysonia. Somewhat similar basal leaves are developed in three species from the Malabar coast of W. India (here treated as the genus Paracaryopsis: Chapter 18) but these differ considerably in their indumentum. The large leaves of some Solenanthus species differ not only in indumentum but also in venation pattern.

The venation pattern in Tysonia can be interpreted as a development from that prevailing in Paracynoglossum. The midrib and the 6-12 lateral veins are depressed on the upper surface and prominent beneath, as in many species of that genus, but their indumentum is not noticeably denser than that of the rest of the lamina.

The indumentum of the basal leaves in all species is minutely puberulous to strigillose. T. africana (Fig. 22.1) has a shorter, sparser and more randomly adpressed indumentum than either T. glochidiata or T. campanulata. In T. glochidiata (Fig. 22.2) the upper surface is rather sparsely setulose, the hairs antrorse and angled outwards from the midrib, while the lower surface is densely strigillose, the hairs slightly longer than on the upper surface and retrorsely adpressed, directed inwards towards the midrib. Multicellular tubercles, similar to those of Cynoglossum, Paracaryum etc., occur, especially on the basal leaves and bracts, but not all hairs possess them (especially in T. glochidiata).

The cauline leaves are lanceolate to narrowly elliptic, with 3-5 principal veins. The indumentum is similar to but ± denser than that of the basal leaves. Multicellular tubercles appear to be absent in T. africana, but in the other two species they are present on the upper (and rarely the lower) surface in at least some populations. As in other genera, the degree of their development is to some extent affected by environment but they always appear best developed on the upper surface, where a small percentage of the setiform hairs often arise from bases surrounded by 2 rings of subsidiary cells.

22.3.3 Inflorescence:

The impressive, large, loosely paniculate, many-flowered inflorescence, common to all species of Tysonia, is unknown elsewhere in the Cynoglosseae. The three species differ in the degree and mode of branching, and in the morphology of the bracts.

In T. africana, each branch of the inflorescence develops into a terminal cyme or pair of cymes; secondary branches are present but relatively few. T. campanulata is similar but lacks secondary branches. In T. glochidiata, branching is more complex, the longer and more slender branches giving off several pedunculate cymes. The inflorescence (but not the individual flowers) is bracteate. The position of the bracts, particularly in T. glochidiata and T. africana, is unusual. Instead of the branches and peduncles arising from the axil of a bract (the usual condition in other bracteate taxa of Cynoglosseae except for Austrocynoglossum latifolium) the nodes, except the lowest, are normally bractless. Each inflorescence branch, however, possesses a single linear-lanceolate bract of the first order, which arises on its abaxial side. Similarly, the peduncle of each cyme in T. glochidiata bears a similar, smaller, linear or lanceolate-linear second-order bract. The position of the bracts may be of taxonomic value at the specific level. In T. africana they develop either near the distal

end of the branch, just below the first formed flower of the cyme, or about half-way along the branch, while in T. glochidiata they arise in the lowest ⅓ of the branch or peduncle, nearest the node. T. campanulata differs from the other species by its much larger, leaf-like lower bracts which arise at the base of the subtended branch or peduncle (Fig. 22.3) but the upper first-order bracts and the second-order bracts are similar to those of the other two species in morphology and position.

22.3.4 Calyx:

The deeply lobed calyx is scarcely accrescent in fruit and broadly similar to that of Cynoglossum. The strigillose indumentum is greyish, often with a bluish tinge.

22.3.5 Corolla:

The corolla is subrotate to shortly campanulate in T. africana and T. glochidiata but distinctly campanulate with an elongate tube in T. campanulata. The patent to subreflexed lobes are a distinctive, unusual feature, unknown in related genera. They are best developed in T. africana and T. glochidiata; in T. campanulata they are shorter, less reflexed and somewhat thickened. All species have exserted stamens and ± exserted style, but there are taxonomically important differences in the degree of exsertion. Considerably exserted stamens and style are characteristic of T. africana and T. glochidiata; in T. campanulata the anthers only just surpass the corolla throat and the style is at first included, becoming equal to and finally (after anthesis) slightly longer than the corolla. In all species the filaments and style appear to develop at a similar rate and are about the same length at anthesis (the style sometimes being shorter, especially in T. campanulata). The versatile anthers are characteristic of all species and seem to represent an independent, parallel trend to that found in Solenanthus. The long dark filaments have peculiar, flattened but dilated bases; these are best developed in T. africana and T. glochidiata.

The

The corolla scales vary in morphology and can be used to separate T. campanulata from the two southern species, T. africana and T. glochidiata. In the latter, they are large, trapeziform to triangular-oblong, with dense papillae on the margin and apical region (Fig. 22.2), and considerably overtop the corolla throat. In T. campanulata, they are reduced to compressed-triangular or semilunar thickened folds, lacking papillae, but are still exserted from the top of the throat (Fig. 22.3).

The corolla colour has been variously described as yellow, creamy, white or white with a mauvish tube. Bolus described the colour of T. africana as yellow; it is possible that he was describing the colour when dry, since Hilliard, Burtt & Shirley (in sched., H. 11210) said that the corolla was white with a mauvish tinge. This is similar to the colour recorded for T. glochidiata by TRAUSELD (1969 and in sched.). The scales of T. glochidiata are creamy, becoming brownish and much darker than the corolla lobes on drying.

No pollination data have been traced in the literature. The combination of white to cream corolla with well developed basal nectaries, patent to subreflexed lobes to serve as a landing platform, and exserted style and stamens, suggests that T. glochidiata and T. africana may be pollinated by relatively short-tongued moths. The campanulate corolla of T. campanulata appears to be adapted to another type of pollination agent, but retains many of the characters of T. africana and T. glochidiata, albeit in reduced form.

22.3.6 Nutlets:

The differences in the nutlet morphology between T. africana and T. glochidiata have been outlined above (Fig. 22.2). The seemingly great difference between the two species in regard to nutlet morphology is difficult to reconcile, especially since the distinction between winged, non-glochidiate nutlets and wingless, glochidiate nutlets has normally been considered fundamental to Cynoglosseae taxonomy. To find both types in one genus

is therefore of great significance, especially as the two species concerned are so closely related by all other characters. This close relationship renders their separation into two genera wholly unthinkable, even though if the traditional 'rules' concerning generic limits were applied this would be the normal decision. The difference is such that it warrants the rank of section, but as the genus is so small, and since the nutlets of the third species, T. campanulata, are unknown, the interpolation of a rank between genus and species would serve no practical purpose. The situation in Tysonia is analogous to that found in Pardoglossum; discussions of the taxonomic implications are found in the account of that genus (sect. 14.1) and in sect. 2.5.3).

22.4 PALYNOLOGY

Pollen of T. africana and T. glochidiata has been examined, apparently for the first time. Quantitative results are summarised in Table 22.1.

Description:

Pollen small to medium, not exceeding 17 μm, oblong, with or without equatorial constriction, if present, moderate to very weak (C = 97-89); heterocolpate, tricolporate, tripseudoapertures included, apertures zonotreme. Amb hexagonal, appearing circular, goniotreme. P = 12-17 μm; E = 6.5-10 μm; B = 8-11.5 μm; D = 8-12.5 μm. P/E = 1.48-1.75, P/B = 1.43-1.55 (pollen prolate). Ectoapertures narrowly rhombic colpi, ± bordered by bacula and ± indistinct furrow; endoaperture a lalongate endocolpus; pseudocolpi similar or ± dissimilar to colpi, narrowly oblong-rhombic. Collar present but incomplete. Sexine granular to finely reticulate, the texture rendering observation of colpi difficult. NPC = 345.

1. Equatorial constriction absent or very weak (C = 100-97);
   P/E = 1.48, P/B = 1.43; sexine finely reticulate ..... africana
1. Equatorial constriction distinct, moderate to weak (C = 94-89);
   P/E = 1.71-1.73, P/B = 1.52-1.55; sexine granular ..... glochidiata

Material examined:

T. africana H. Bolus (Natal, Polela, Wood 973!).

T. glochidiata R. Mill (Natal, Alfred Distr., Weza, Zuurberg, Hilliard 5487 (holo. E!); Estcourt Distr., Giant's Castle Reserve, Trauseld 562! ibid., McKeown 107!

Discussion:

In shape, the pollen of Tysonia is somewhat similar to that found in Paracynoglossum (but distinguished by its larger size). That of T. africana, especially, resembles the African members of that genus. The pollen is totally unlike that of any species of Rindera, Solenanthus or Caccinia - the genera to which Bolus related T. africana. Though dumb-bell shaped, the equatorial constriction is not nearly as pronounced as in the three Indian species of Paracaryopsis which have somewhat similar basal leaves to Tysonia; moreover, the pollen of that genus is half the size of that of Tysonia, with a very much higher range of P/E values (always exceeding 2.00).

Within-species variation of Tysonia pollen is very small, especially in regard to P/E and P/B. In T. glochidiata, the pollen of the type specimen (Hilliard 5487) is noticeably smaller than the other preparations, but the difference may not be taxonomically significant.

Within the genus, the pollen of T. glochidiata has the greater degree of equatorial constriction and therefore, if trend follows the same direction as in the group of genera centred on Cynoglossum, its pollen must be reckoned as more derived. Such a direction appears to be more probable than the reverse, and would allow the reticulate sexine of T. africana to be considered 'primitive' (a sexine of this type is unknown in Cynoglossum, which is characterised by a smooth sexine). The relatively large pollen also indicates that Tysonia is not particularly advanced palynologically. The incomplete equatorial collar is analogous to that of African members of Paracynoglossum and supports an affinity with the Cynoglossum group.

Table 22.1

Quantitative Palynological Characters of *Tysonia*

Species	Specimen	C	P µm	E µm	B µm	D µm	P/E	P/B
africana	Wood 973	97	13.8 (12.9-14.4)	9.3 (8.7-10.0)	9.6 (9.1-10.2)	10.5 (10.0-11.3)	1.48	1.43
glochidiata	Trauseld 562	89	15.4 (14.0-16.0)	9.0 (8.7-9.4)	10.1 (9.4-10.7)	10.2 (9.1-11.3)	1.71	1.52
	McKeown 107	90	15.7 (15.0-16.9)	9.1 (8.7-9.8)	10.1 (9.4-11.3)	11.1 (10.0-12.5)	1.73	1.55
	Hilliard 5487	94	13.7 (12.5-15.0)	7.9 (6.5-8.7)	9.0 (7.8-9.4)	9.6 (8.2-10.6)	1.73	1.52
	Mean	91	14.9	8.6	9.7	10.3	1.72	1.33
	Range		12.5-16.9	6.5-9.8	7.8-11.3	8.2-12.5	1.71-1.73	1.52-1.53

Sample size: 10 grains in equatorial view, 10 in polar view, from each specimen

C = index of constriction P = length of polar axis B = maximum breadth

D = polar diameter E = equatorial diameter P/E = Erdtman's ratio

22.5 RELATIONSHIPS

BOLUS (1890) believed Tysonia to be 'allied to Caccinia, Solenanthus and more nearly to Rindera' but added that he had 'no access' to other figures or specimens of Rindera. He also observed that the leaves, habit and nutlet shape were very similar to the New Zealand species Myosotidium hortensia, but noted strong differences between Myosotidium and Tysonia in the probably more taxonomically significant characters of flower, fruit and cotyledons.

The present research indicates that the genus is most nearly related to Paracynoglossum, with which it shows strong palynological agreement, but that its relations with that genus are not close. The corolla can be interpreted as a derivative of Cynoglossum-type stock. The cauline leaves are broadly similar to those of African Paracynoglossum, but the basal ones are markedly different. T. glochidiata has nutlets very similar to Cynoglossum, although T. africana, with its specialised winged nutlets, lacking glochids and often solitary by abortion, is very different.

Apart from the large basal leaves, the principal differences from Cynoglossum and Paracynoglossum common to all species of Tysonia are the patent to reflexed corolla lobes, the versatile medifixed anthers ± exserted on long filaments, the ± exserted style, the strongly developed, horned basal nectaries and the very large paniculate inflorescence with its peculiar arrangement of bracts and bracteoles. These combined merit the recognition of Tysonia as a very distinct, natural genus of somewhat isolated affinity. It is uncertain whether Tysonia is more or less advanced than Paracynoglossum, but the evidence from floral morphology and palynology suggests that it is a specialised and probably recent derivative from Cynoglossoid stock, which has become adapted to a specific, possibly lepidopteran pollinator. More species may remain to be discovered.

There are no relations whatever with any of the genera which Bolus suggested as congeners. Solenanthus, although having versatile anthers,

differs markedly in palynology and floral morphology. It represents a totally different line, but also arising from (Asian) Cynoglossoid stock. Rindera differs in habit, inflorescence, floral morphology and very markedly in palynology; the structure of the wing in T. africana is also different to that of Rindera. Ceccinia (not treated in this thesis) is unrelated to any genus of Cynoglosseae and has been removed from that tribe to the tribe Trichodesmeae (cf. RIEDL 1967, and other recent authors).

CHAPTER 23

15. AUSTROCYNOGLOSSUM M. Popov ex R. Mill

23.1 INTRODUCTION

Austrocynoglossum is a monotypic Australian genus. Its single species, A. latifolium (R. Br.) R. Mill, originally described as Cynoglossum latifolium R. Br. by BROWN (1810), is a forest herb widely distributed throughout Victoria, New South Wales, S. Australia and Queensland; it also occurs in Tasmania (Map 23.1).

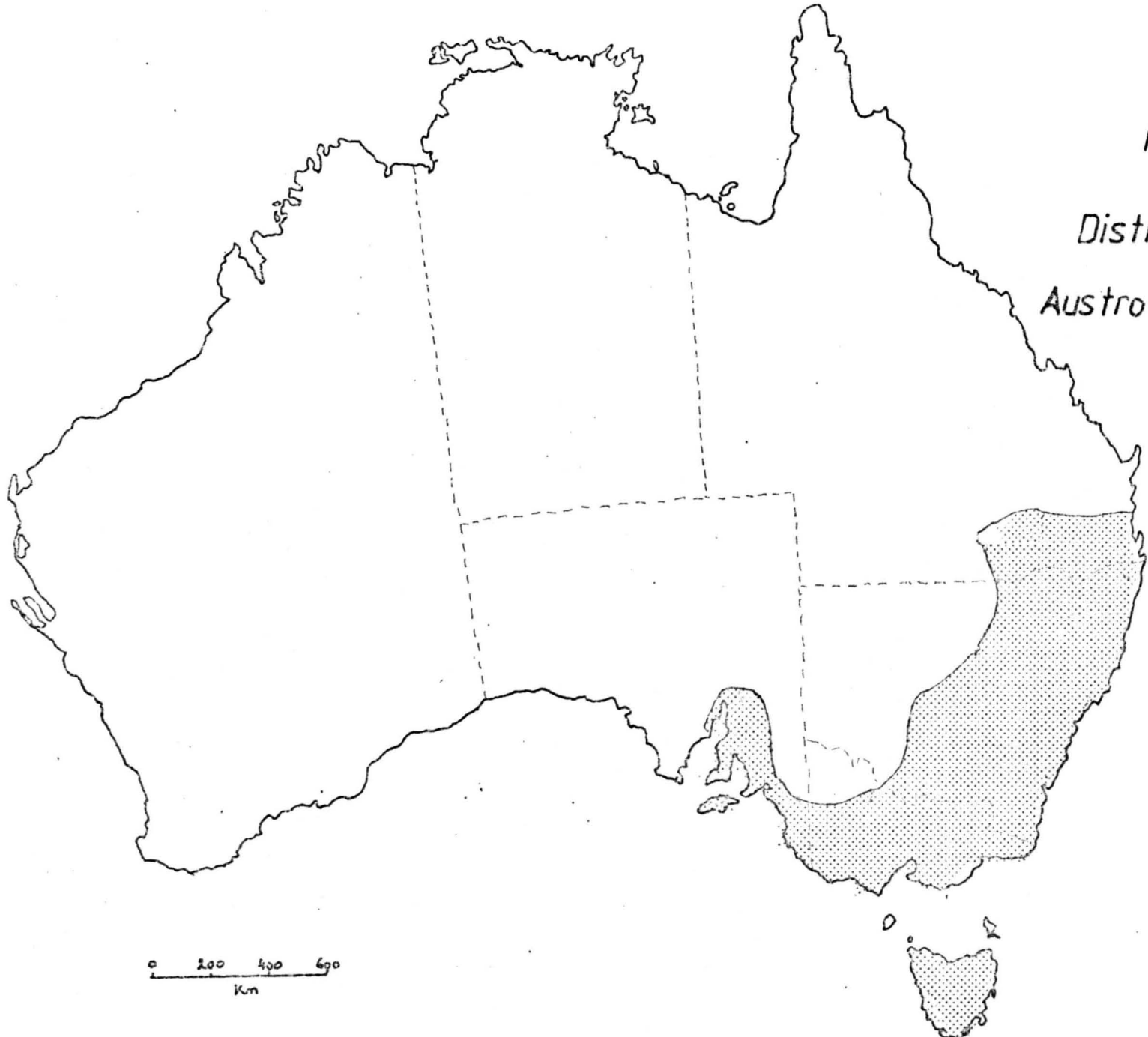
In his account of Cynoglossum for Flora URSS (op. cit. 658, 1953), POPOV observed '... the Australian C. latifolium R. Br. is unquestionably a separate genus, Austrocynoglossum M. Popov'. The genus was not described, however, and Popov's name has remained a nomen nudum. As the evidence I have obtained from morphological and palynological studies strongly supports Popov's view, I take this opportunity of providing a formal account of the genus here.

23.2 SYSTEMATIC TREATMENT

Austrocynoglossum M. Popov ex R. Mill, gen. nov.

Type: A. latifolium (R. Br.) R. Mill, comb. nov. Syn: Cynoglossum latifolium R. Br., Prodr. Fl. Nov. Holl. 496 (1810). Fig. 23.1

Herba perennis effusa. Caules debiles tenues ramosi, ad metra compluria longi, ± compressi, ± striati, tuberculis remotis magnis praediti, tuberculi setulos aculeiformes robustos retroflexos plerumque ferentes, mox calcarati; setae 0.5-1 mm longae, e basi amplo celeriter angustatae. Folia basalia absentia. Internodia caulina longa (ad 3 cm), folia alterna, unumquidque saepe folio multo minore in axillo ferens, omnia (suprema excepta) petiolata, suprema petiolo reducto, basi alato. Petiola foliorum medianorum 10-15(-18) mm, superiorum (floralium) (0-)5-10 mm, omnia alata, marginibus alarum aculeos retroflexos ferentibus. Lamina ovata usque late lanceolata, integra,



Map 23,1

Distribution of

Austrocynoglossum

mucronata, mediana 40-60 x 20-35 mm basi subtruncato vel obtuso, abrupte in petiolum alatum attenuato; venatio camptodroma, venis principalibus longitudinalibus 5-7, in parte tertia inferiora laminae omnis exorientibus, subtus prominenter elevatis. Folia superne tuberculis magnis multicellularibus calcaratis praedita, cellula tuberculorum oblongo-hexagonalia annulos (1-)2(-3) concentricos irregulares formantia, primo hyalina deinde mox albescentia; tuberculi setulos brevissimos ferentes. Lamina inferne glaberrima secus nervos elevatos sparse aculeatos excepta.

Flores solitaria, ad vel parum infra insertionem uniuscuiusque folii superioris exorientia. Pedicelli longissimi filiformes in caulem decurrentes, in statu fructifero valde elongati, pilis ± densis antrorsis adpressis et aculeis remotis paucis praediti. Calyx ad 4/5 divisus, in statu fructifero parum accrescens, lobi ovati integri acuti, pars inferiora indivisa receptacularis densissime pilosa, lobi extus sparsissime pilosi intus glabri. Corolla caerulea vel alba, breviter campanulata, 2-3.5 mm longa, tubus limbum subaequans, limbus ad faucem leviter expansus, ad basem divisus, lobi late elliptici-oblongi, subtruncati, obtusissimi, paulo longiores quam lati. Fornices humiles, late triangulares ad semilunares, leviter emarginati, c. 0.1-0.3 mm alti, 0.3-0.7 mm lati, latitudinem loborum aequantes, tota papillosa. Filamenta brevissima. Antherae oblongo-ovoideae, c. 0.2-0.3 x 0.15-0.2 mm, in medio tubi insertae, apicibus bases fornicium non attingentibus. Annulus absens. Stylus brevis, c. 0.5 mm longus, stigma capitatus. Nuculae 4, ad gynobasem areola prismatico-triangulare parva super funiculum brevem c. 1 mm diam. affixae, obovatae, c. 2.5-3 x 1.5-2 mm, facies ventralis glabra, dorsalis convexa ± compressa immarginata, dense glochidiato-aculeata, glochidibus 0.5-0.7 mm longis.

Straggling perennial herb. Stems weak, slender, extending to several metres, branched, somewhat flattened, ± striate, with rather remote large tubercles which usually develop into strong retrorse prickle-like setae; tubercles becoming calcified; setae rapidly tapering from a broad base,

0.5-1 mm long. Basal leaves absent. Cauline internodes long (to 3 cm), leaves alternate, all ± petiolate (uppermost with petiole reduced to a winged leaf base), each leaf often with a much smaller one in its axil. Petioles of median leaves 10-15(-18) mm, of upper (floral) leaves (0-) 5-10 mm, all winged, with retrorse prickles along the wing margins. Lamina ovate to broadly lanceolate, entire, mucronate, median 40-60 x 20-35 mm; base obtuse to subtruncate, abruptly changing into winged petiole; venation camptodromous, longitudinal veins 5-7, prominently raised beneath and bearing short stout prickles, all main veins arising in lower ⅓ of leaf. Upper surface of leaves sparingly covered with large multicellular calcifying tubercles, the cells oblong-hexagonal, in (1-)2(-3) concentric rings, hyaline at first but quickly becoming white; tubercles bearing minute stubby trichomes; lower surface completely glabrous except on veins.

Flowers solitary, arising at or slightly below each upper leaf. Pedicels long, filiform, decurrent on to stem, with ± dense antrorsely adpressed setules and few retrorse prickles, greatly elongating in fruit. Calyx divided to 4/5, slightly accrescent in fruit, lobes ovate or broadly ovate, entire, acute, densely hairy on undivided receptacular portion, much more sparsely hairy on lobes outside, glabrous inside. Corolla blue or white, shortly campanulate, c. 2-3.5 mm long; tube subequal to limb; limb slightly expanded at throat, divided to base into 5 broadly elliptic-oblong subtruncate or very obtuse lobes slightly broader than long. Faucal scales small, triangular or semilunar, slightly emarginate, c. 0.1-0.3 x 0.3-0.7 mm, as broad as lobes, papillate all over. Filaments very short. Anthers oblong-ovoid, c.0.2-0.3 x 0.15-0.2 mm, inserted in middle of tube, their apices not reaching bases of scales. Annulus absent. Style short, c. 0.5 mm, stigma capitate. Nutlets 4, attached to gynobase by small prismatic-triangular apical scar on short funicle c. 1 mm diam., obovate, c. 2.5-3 x 1.5-2 mm, ventral surface strongly developed, glabrous; dorsal surface convex,

Figure 23.1

Austrocynoglossum latifolium: Morphology

(All drawn from Morrison 25 i 1896)

1 Middle cauline leaf, upper surface, x 0.87

2 Upper cauline leaf, lower surface, x 0.87

3 Upper surface indumentum, x 35

4 Lower surface indumentum, x 35

5 Upper surface trichome, x 85

6 Lower surface trichome, x 85

7 Indumentum of leaf margin, x 35

8 Inflorescence, x 0.87, showing pedicels arising below bract axils

9 Stem indumentum, x 8.7

10 Calyx, x 4.4

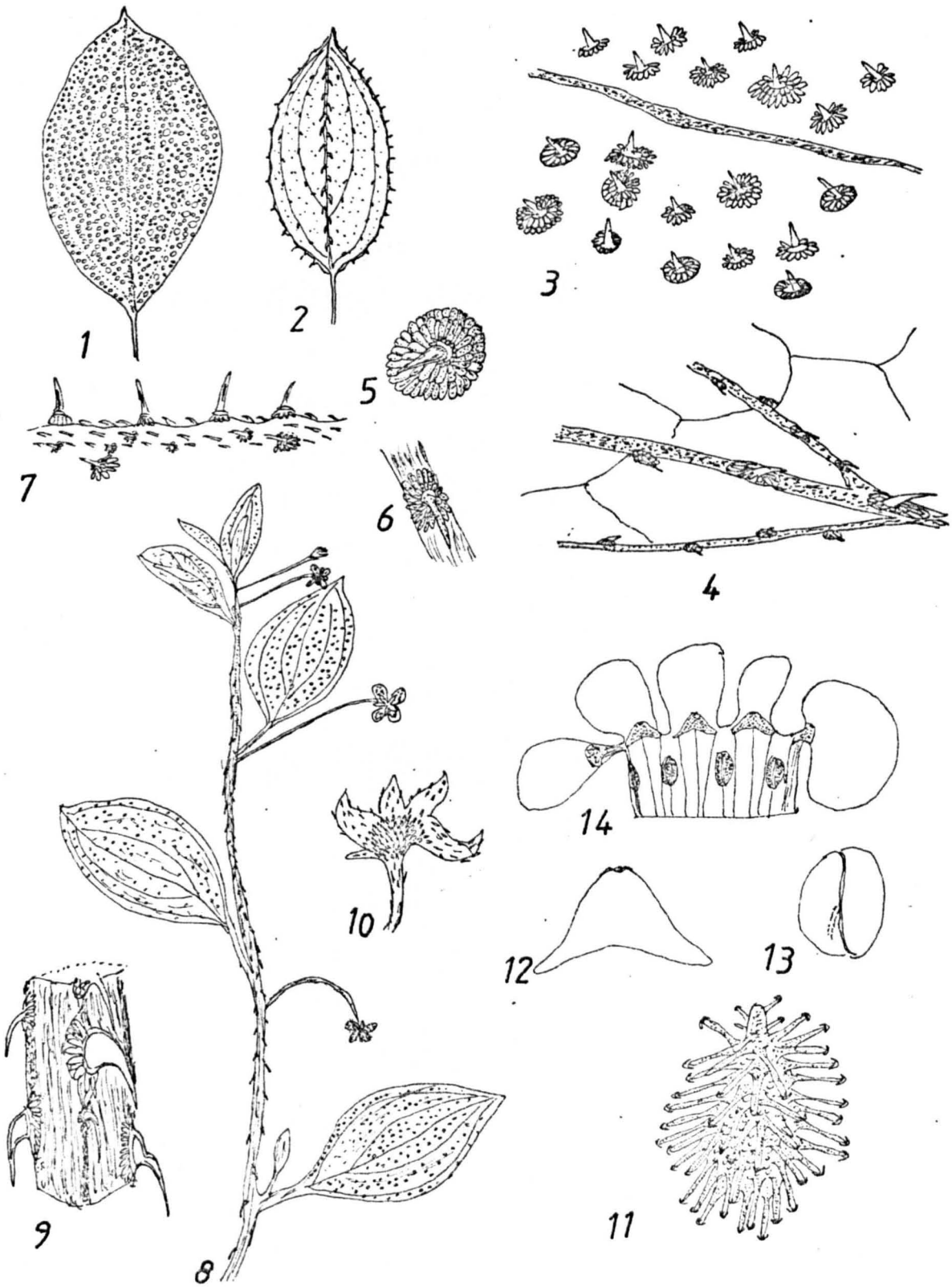
11 Nutlet, x 17.5

12 Faucal scale, x 45

13 Anther, x 87

14 Corolla opened out, x 8.7

Figure 23,1



somewhat flattened, immarginate, evenly and densely glochidiate-aculeate, glochids 0.5-0.7 mm long.

23.3 MORPHOLOGY AND RELATIONSHIPS

Austrocynoglossum is very distinct morphologically and in its general facies and habit is quite unlike any species of Cynoglossum or Paracynoglossum, including the three Australian species of the latter genus, although it approaches the latter genus in floral morphology. Several aspects of its morphology are clearly adaptations to its forest habitat, e.g. the large dark green leaves with only thinly scattered tubercles (cf. Cynoglossum germanicum), the straggling habit with stems up to a metre or more long which cling to neighbouring vegetation by means of the retrorse prickle-like setules, and the indeterminate inflorescence of solitary flowers borne below the leaf-like bracts. This type of inflorescence is unknown in either Paracynoglossum or Cynoglossum.

In many floral characters, especially corolla shape, form of faucal scales, and form and insertion of anthers, A. latifolium is close to Paracynoglossum. It differs from Paracynoglossum, however, by the nutlet attachment. The development of a short obconical funicle is not known in Cynoglossum and rare in Paracynoglossum. The reduced attachment scar at the apex of the funicle also differs from the normal situation in Cynoglossum and Paracynoglossum, where the attachment scar usually occupies a large part of the ventral surface. The nutlets are free from the style, indicating a greater affinity with Paracynoglossum, but there is no basal extension of the style to form an elevated gynobase. The minute style is in fact hidden by the nutlets, creating a condition reminiscent of Omphalodes.

Austrocynoglossum appears to hold an isolated position in the Cynoglosseae. There is no affinity with the Australian species of Paracynoglossum, nor with the Malaysian and Indonesian ones. Perhaps the nearest relatives in

that genus are the S. American P. trianaeum and P. limense, but the relationship is very distant. There is some similarity to Mimophytum, especially in leaf shape, but this is not an indication of relationship, rather of parallel evolution. The lack of close relationships with other genera, together with its many distinctive features, are sufficient to warrant the recognition of Austrocynoglossum as an independent genus.

23.4 PALYNOLOGY

The following is apparently the first description of the pollen of A. latifolium.

Material examined: Australia: Victoria, Ferntree Gully, 25 i 1896, A. Morrison! Waterloo, iv 1894, L. Walker!

23.4.1 Description:

Pollen oblong, dumb-bell shaped, equatorial constriction moderate (C = 84); heterocolpate, tricolporate, tripseudocolpate, with little distinction between colpi and pseudocolpi. Amb hexagonal, straight, acute, appearing ± peritreme, pseudoapertures included. P = 13.5 (13.2-14.0) µm, E = 6.0 (5.5-7.0) µm, B = 7.1 (6.7-7.4) µm, D = 7.2 (7.0-7.4) µm. P/E = 2.25; P/B = 1.90 (prolate). Colpi linear, bordered by furrow; endoapertures an endoporus; pseudocolpi linear, bordered by furrow. Collar absent. NPC = 345. Sexine smooth.

23.4.2 Discussion:

A. latifolium was formerly included in Cynoglossum sect. Eleutherostylum by BRAND (1921). There is no close palynological similarity with any species included by him in that section, and none whatever with the genus Eleutherostylum as delimited here. RIEDL (1962) transferred A. latifolium to Cynoglossum subgen. Paracynoglossum (M. Popov) H. Riedl, here treated as the genus Paracynoglossum M. Popov.

The pollen of A. latifolium is similar to that of Paracynoglossum in

general morphology but is appreciably larger than is usual in that genus. Only the pollen of P. amplifolium approaches it in size, but A. latifolium differs by the complete absence of an equatorial collar and by the higher P/E and P/B ratios. The latter are among the highest recorded in my research, comparable only with certain species of Paracaryopsis, Mimophytum and Omphalodes, and with sect. Latifolia of Paracynoglossum. In these taxa, however, the pollen is much smaller. The combination of relatively large grains with very high P/E and P/B ratios is only found in A. latifolium and supports the morphological evidence for its separation as a genus.

23.5 CHEMOTAXONOMY

Alkaloids:

Three distinctive alkaloids have been reported from A. latifolium by CROWLEY & CULVENOR (1962):

latifoline ($C_{20}H_{27}NO_7$);

latifoline N-oxide ($C_{20}H_{27}NO_8$);

7-angelyl-retronecine ($C_{13}H_{19}NO_3$).

All these alkaloids are unique to A. latifolium and are structurally unlike the Cynoglossum and Paracynoglossum alkaloids (cf. CULVENOR 1978). Chemical research therefore furnishes additional evidence in support of the generic separation of A. latifolium. The alkaloid 7-angelyl-retronecine has the same formula but a different structure to the Heliotropium alkaloid 7-angelyl-heliotridine, which has not been recorded from the Cynoglosseae. The $C_{20}H_{27}NO_7$ structure of latifoline is apparently also unknown elsewhere in the Cynoglosseae.

CHAPTER 24

16. OMPHALODES Miller

24.1 INTRODUCTION

The genus Omphalodes as here defined comprises 14 species centred in the Mediterranean area and Caucasia (Map 24.1). Several Mexican, Japanese, Chinese and American species described under Omphalodes are here excluded from the genus.

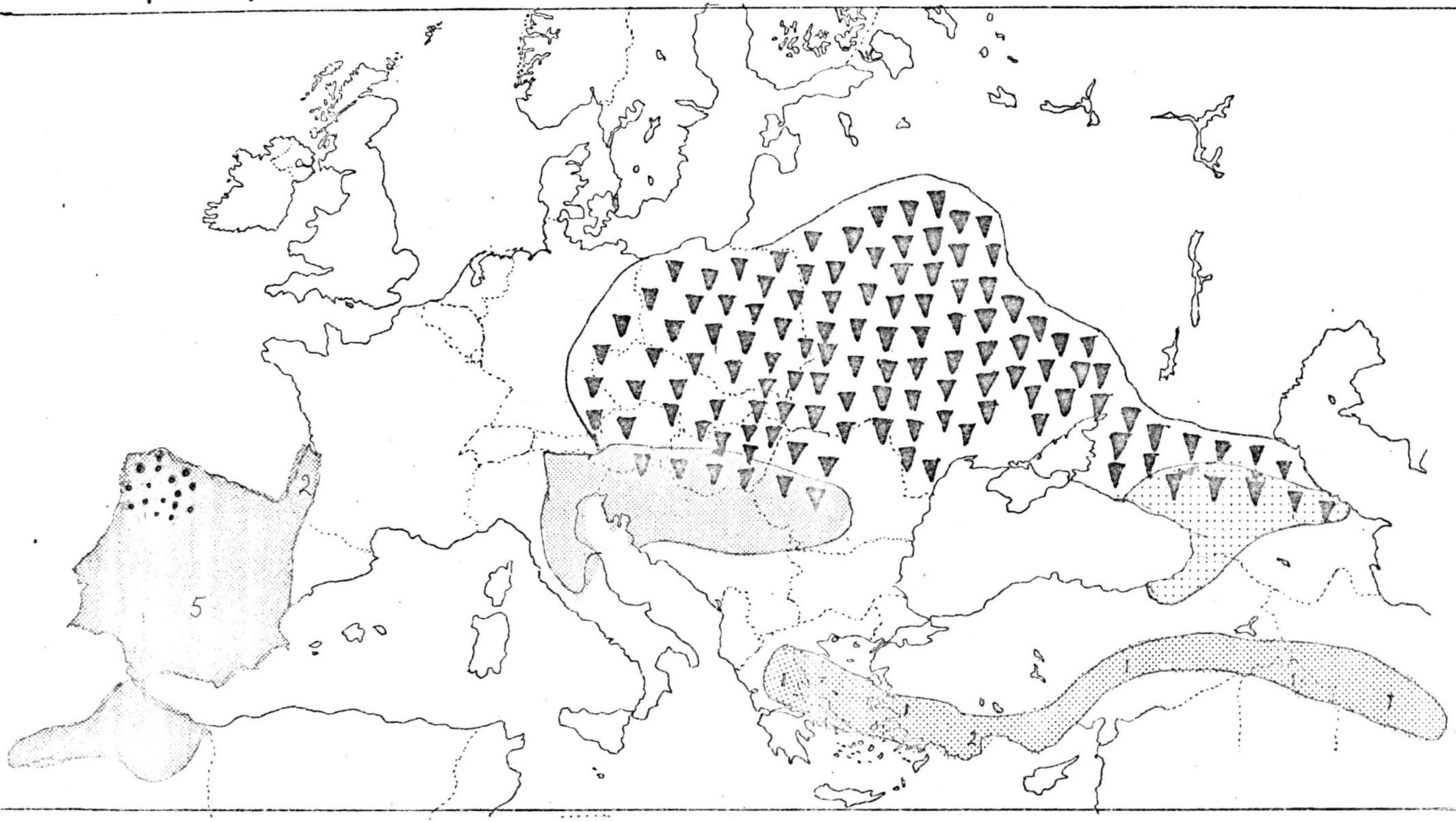
Omphalodes was first conceived as a genus distinct from Cynoglossum by TOURNEFORT (1700). He described two taxa, which he named O. Lusitanica elatior, cynoglossi folio (= O. nitida Hoffmans. & Link) and O. Lusitanica, Lini folio (= O. linifolia (L.) Moench). Three years later (TOURNEFORT 1703) he described a third species, O. Orientalis, Corni folio which was validly published as Cynoglossum cappadocicum by WILLDENOW (1797) and transferred to Omphalodes by DE CANDOLLE (1846).

MILLER (1752, 1754) also originally recognised Omphalodes as a distinct genus and appears to be the first author to mention the species now known as O. verna Moench. Since the abridged edition (1754) of the 'Gardener's Dictionary' contains an adequate generic description which is valid under the rules of the International Code of Botanical Nomenclature (STAFLEU et al./1978), the authorship of the genus should correctly be attributed to Miller and not to MOENCH (1794). Despite papers by DRUCE (1913), DANDY & STEARN (1960) and INGRAM (1961) drawing attention to this fact, many Floras (e.g. POPOV 1953 and RIEDL 1967) still incorrectly credit Moench with the first valid publication of Omphalodes.

LINNAEUS (1742), however, had a broader generic concept and included Omphalodes in his genus Cynoglossum. He maintained this view in the 'Species Plantarum' (1753), treating Tournefort's Omphalodes Lusitanica elatior, cynoglossi folio as a variety of his Cynoglossum linifolium. He also described a second species, C. omphaloides, which is conspecific with the

Map 24,1

Distribution of Omphalodes



● Subsect. Nitidae

Subgen. Maschalanthus

Sect. Cordollea

Subsect. Omphalodes

Subsect. Caucasicae

Subsect. Lucilianthe

species described under the polynomial Omphalodes verna ... by MILLER (1752, 1754). He was, however, apparently unaware of Miller's work as he cited in synonymy only polynomials of Bauhin and Morison. He retained this broad generic concept throughout his work, although later (LINNAEUS 1764) he added the following note:

'Omphalodes T(ournefort) 5, 6, 7. arillis, nec echinato-hamosis differt'. The considerable difference in nutlet structure which lies behind this terse note was nevertheless insufficient to influence LAMARCK (1786) or SCHREBER (1789) in their respective treatments, and even MILLER (1768) adopted Linnaeus' broader view of Cynoglossum in later editions of his work.

MOENCH (1794), however, disagreed with Linnaeus'broad generic concept and re-instated Omphalodes as a distinct genus, consisting of two species, O. verna Moench and O. linifolia (L.) Moench. WILLDENOW (1797) followed in the Linnaean tradition in describing Cynoglossum cappadocicum.

DE CANDOLLE (1846) recognised Omphalodes and considerably broadened its limits through transfers of species from other genera and by the description of several new species. The De Candollean genus must today be considered very heterogeneous. He recognised 4 sections:

Sect. 1 Pseudanchusa DC., Prodr. 10: 158 - monotypic, O. longiflora (Bentham) DC. (= Lindelofia longiflora (Bentham) Baillon).

Sect. 2 Paracaryum DC., op. cit. 159

- Grex 1 calyx non accrescens nuculis maturis brevior: 7 species later elevated to generic rank as Paracaryum (DC.) Boiss. (BOISSIER 1849).
- Grex 2 calyx accrescens nuculis maturis longior aut eas subaequans: 3 species - O. amplexicaulis Lehm. (= O. brassicifolia (Lag.) Lehm.), O. littoralis Lehm., O. linifolia (L.) Moench.

Sect. 3 Maschalanthus A. DC. in DC., op. cit. 161: monotypic, comprising O. scorpioides (Haenke) Schrank

Sect. 4 Euomphalodes A.DC. in DC., op. cit. 161: 4 species - O. nitida Hoffmans. & Link, O. cappadocica (Willd.) DC., O. luciliae Boiss., and O. verna Moench.

MAXIMOWICZ (1872) further broadened the generic limits by recombining Cynoglossum japonicum Thunb. and describing as new under sect. Eucomphalodes the Japanese species O. sericea Maxim. The latter was transferred by JOHNSTON (1940) to the genus Trigonotis as a synonym of T. radicans. Due to a misunderstanding of the generic characters and to evolutionary convergence resulting in remarkable but superficial similarities to the European species of Omphalodes, many other taxa from E. Asia have been, and still are being wrongly described under Omphalodes (as by FRANCHET & SAVATIER 1875, 1879, FRANCHET 1887, MAXIMOWICZ 1880, 1881, DIELS 1912, BRAND 1915, 1921, 1929, LEVEILLE 1913, MASAMUNE 1930, MIGO 1942, RECHINGER fil. & H. RIEDL in RIEDL 1963a). Indeed, the limits of Omphalodes with other genera from the Far East were so poorly understood that one species (O. bodinieri Levl., 1913) was actually found by HANDEL-MAZZETTI (1920) to belong not to the Boraginaceae but to the Loganiaceae, where it is a synonym of Mitreola pedicellata. Most of the incorrectly assigned taxa from the Far East have since been referred to Microula, Antiotrema, Trigonotis and other genera by Johnston and other workers. Three Japanese species - O. japonica, O. krameri and O. prolifera - are here considered to have no real affinity with Omphalodes but to represent a new genus, Desmolopha R. Mill (Chapter 25). The few other new combinations still apparently necessary are given below as part of a full list of excluded taxa.

Several Mexican taxa have also been included in Omphalodes. In the present account they are all transferred to the genus Mimophytum Greenman, except for O. erecta Johnston, which is considered sufficiently distinct to warrant its recognition at generic rank as the genus Madrea R. Mill. The reasons for these transfers are discussed under the relevant genera (Chapters 19 and 26).

The removal of the three Japanese species and the six Mexican ones, along with the referral of two East Asian species to Trigonotis and the transfer of O. heterophylla Rech. fil. & H. Riedl to Lepechiniella on account of its

nutlet structure, leaves Omphalodes as a relatively natural genus of 14 species centred in S.W. Asia and Caucasia, with a secondary centre of diversity in the W. Mediterranean (especially the Iberian peninsula).

Two nomenclatural points must be noted:

1. O. lusitanica auct. is based on O. Lusitanica, elatior, cynoglossi folio of TOURNEFORT (1700), which Linnaeus incorrectly considered to be a variety of his Cynoglossum linifolium (O. linifolium (L.) Moench) which has white flowers. Thus, as DANDY & STEARN (1960) and INGRAM (1960) have observed, it must not be used for the Portuguese species with deep blue flowers correctly known as O. nitida Hoffmans. & Link.

2. The Spanish and N. African species first named Cynoglossum brassicaefolium Lagasca was validly transferred to Omphalodes by LEHMANN (Asperif. 185, 1818) and the combination O. brassicaefolia (Lag.) Lehm. was taken up by ROEMER & SCHULTES (1819). These references antedate by 8-9 years the publication of SWEET's 'Hortus Britannicus' (1827), which has hitherto been taken as the place of first valid publication of the epithet. Under Article 73.10 of the International Code of Botanical Nomenclature (STAFLEU et al. 1978), the spelling of the specific epithet should be altered to 'brassicifolia'. Thus the correct citation should read O. brassicifolia (Lag.) Lehm., not O. brassicifolia (Lag.) Sweet as frequently cited. This note makes a correction necessary to Flora Europaea 3 (TUTIN et al. 1972).

DE CANDOLLE (1846) was the first author to subdivide Omphalodes; his classification has already been outlined. The differential characters which he used to separate his sections Paracaryum, Euomphalodes and Maschalanthus are briefly tabulated below.

Paracaryum	Maschalanthus	Euomphalodes
'Nuculae stylo pyramidato quadrangulari lateraliter et longe affixae'.	'Nuculae turbinato-depressae basi vix lateraliter puncto stylo persistente libero maiore'.	'Nuculae depressae stylo persistente breviores, eo vix basi adhaerentes'.
'Semen pendens'.	'Semen ex angulo interiori oblique adscendens'.	'Semen ex angulo interiori horizontalis'.
'Folia alterna'.	'Folia inferiora opposita'.	'Folia alterna'.
'Pedicelli extraaxillares'.	'Pedicelli axillares'.	'Pedicelli extraaxillares'.

Thus it seems that the essential characters of sect. Euomphalodes are horizontal (i.e. straight) embryo, alternate leaves and depressed nutlets; of sect. Maschalanthus, slightly laterally inserted nutlets with curved embryo, opposite leaves and axillary pedicels; and of the species included in sect. Paracaryum, pendulous ovules, pyramidal gynophore with nutlets attached laterally, and alternate leaves. These characters are still considered important in the classification to be presented below.

MAXIMOWICZ, in describing O. trichocarpa (1880), O. blepharolepis (1881) and O. diffusa (1881) referred them all to sect. Maschalanthus DC. He apparently did this on the strength of the characters of bracteate racemes, axillary pedicels and depressed nutlets, since not one of his type descriptions of these taxa give any details concerning the very important embryo characters. It must therefore be assumed that he did not cut sections of the seed. GÜRKE (1897) however accepted Maximowicz's view of sect. Maschalanthus as a group of 4 species including O. scorpioides. Maximowicz's three species were all transferred to Microula by JOHNSTON (1924b), and later to Anoplocaryum by BRAND (1931). This latter classification has been criticised by POPOV (1953), and by Grierson & Long, who in their current

work on the Flora of Bhutan are including them in Microula (oral communication).

BRAND (1921), in his monograph of Cynoglosseae, recognised 25 species of Omphalodes in two sections, Maschalanthus and Eu-Omphalodes. The latter section, besides including all the species referred to it by De Candolle, also combined De Candolle's sect. Paracaryum and two Japanese species (O. japonica and O. krameri). In addition he included the four Mexican species then recognised having cordate leaves (here referred to Mimophytum) and eight species from the Himalayas, China and Japan, now referred to other genera. Despite the obvious amplifications of both generic and sectional limits implied by this classification, Brand's sectional descriptions are much abbreviated compared to those of De Candolle. The fact that Brand's work is still the standard monograph, despite being outdated, has led not only to taxa being incorrectly described under Omphalodes, but also to incorrect statements as to the limits of Omphalodes, even in recent papers (e.g. GRAU (1967) in the introduction to an important paper on the cytology of the genus, follows Brand in stating that 'in Ostasien ist die Gattung in Japan mit drei, in China mit fünf Arten vertreten' - thus showing ignorance of Johnston's transfers).

POPOV (1953) observed that the genus as then delimited seemed to fall into three groups, centred in Mexico (here = Mimophytum), the Mediterranean and Caucasia, and Japan. He noted that the Japanese species (presumably meaning O. japonica and its allies) 'distinctly differed from the European-Caucasian ... species, representing a special subgenus', but he did not award them a formal subgeneric name. They are here referred to the genus Desmolopha R. Mill (Chapter 25).

Popov was the first person to subdivide sect. Euomphalodes, but in so doing he abandoned De Candolle's sectional name. All his sectional and series names are invalid, as they are supported only by descriptions in Russian. Sect. Arctotertiariae M. Popov would also be illegitimate as it contains O. verna, the lectotype of the genus.

Notwithstanding the nomenclatural shortcomings, Popov's classification was a fair attempt to divide the genus into natural groups. Possibly owing to poor representation in the herbarium, his misunderstanding of extra-Russian species is less satisfactory compared with his grasp of the native taxa.

Sect. Arctotertiariae M. Popov, Fl. URSS 19: 609 (1953) consisted of perennials with large long-petiolate leaves; flowers in differentiated racemiform cymes; gynophore rudimentary, nutlets 'growing mainly laterally ... forming a flat cross on the calyx'. He divided the section into two series:
ser. 1 Vernales M. Popov, op. cit. 609-'Blades of radical leaves narrowly long acuminate, ± coriaceous, lateral nerves protruding; flowers 10-15 mm diam., blue'. (O. verna, O. nitida, O. cappadocica).
ser. 2 Rupestres M.Popov, op. cit. 613 - 'Blades of radical leaves obtuse or acute, mucronate, lateral nerves not distinctly protruding, base not cordate. Flowers large, blue, (10-) 15-20 mm diam.' (O. kusnetzovii, O. lojkae, O. rupestris, O. luciliae).

Sect. Pseudoparacaryum M. Popov, op. cit. 616 is equivalent to O. sect. Paracaryum grex 2 calyx accrescens ... DC. Popov characterised it as comprising ± succulent xerophyllous annuals or biennials with rather high pyramidal gynobase with nutlets forming a pyramid, and listed one adventive species, O. linifolia. Sect. Maschalanthus was recognised as monotypic (O. scorpioides).

While highlighting some useful characters which have been utilised in the following classification, Popov appears not to have fully understood the relationships (or lack of them) between the various species. Especially, his postulated affinities between the species native to the USSR and those of other parts of Eurasia often appear to be incorrect.

I hold the view that Omphalodes is composed of species which with few exceptions are only distantly related to each other. Many of the species possess characters, discussed in the following sections, which suggest that they are of a relict nature. Other species, on the other hand, appear to

be highly derived, and the connecting links between these and less advanced species seem to be no longer extant. I have highlighted these somewhat broken relationships by dividing the genus as here delimited into two subgenera, with subgen. Omphalodes being further divided into two sections, one of which is subdivided into several mono- or oligotypic subsections.

Accepted Taxa:

O. brassicifolia (Lag.) Lehm.

O. cappadocica (Willd.) DC.

O. kusinskyanae Willk. (n.v.).

O. kusnetzovii Kolak. (n.v.).

O. linifolia (L.) Moench

O. littoralis Lehm.

O. lojkae Somm.& Lev.

O. luciliae Boiss.

O. nitida Hoffmans. & Link

O. pavoniana Boiss. (n.v.)

O. ripleyana Davis

O. rupestris Rupr. (n.v.)

O. scorpioides (Haenke) Schrank

O. verna Moench

Excluded Taxa:

O. acuminata Robinson in Proc. Amer. Acad. 26: 170 (1891) = Mimophytum acuminatum (Robinson) R. Mill (sect. 26.2).

O. aliena A. Gray ex Hemsl., Biol. Centr. Amer., Bot. 2: 377 (1882) = Mimophytum alienum (A. Gray) R. Mill (sect. 26.2).

O. amplexicaulis Lehm. in Ges. Nat. Freunde Berlin Mag. 7: 98 t. 3 (1818) = O. brassicifolia (Lag.) Lehm.

O. aquatica Brand in Feddes Rep. 13: 545 (1915) = Trigonotis radicans (Turcz.) Steven (tribe Trigonotideae).

O. blepharolepis Maxim. in Bull. Acad. St. Petersb. 27: 504 (1881) = Microula blepharolepis (Maxim.) Johnston (tribe Eritrichieae).

O. bodinieri Lévl. in Feddes Rep. 12: 188 (1913) = Mitreola pedicellata Bentham (family Loganiaceae).

O. cardiophylla A. Gray ex Hemsl., Biol. Centr. Amer., Bot. 2: 377 (1882) = Mimophytum cardiophyllum (A. Gray) R. Mill (sect. 26.2).

O. cariensis Boiss., Diagn. ser. 1(4): 41 (1844) = Paracaryum lithospermifolium (Lam.) Grande subsp. cariense (Boiss.) R. Mill (sect. 16.2).

O. caucasica Brand in Engler, Pflanzenr. 78 (IV. 252): 109 (1921) = O. cappadocica (Willd.) DC.

O. cavalerei Lévl. in Feddes Rep. 12: 188 (1913) = Trigonotis cavalerei (Lévl.) Hand.-Mazz. (tribe Trigonotideae)

O. chekiangensis Migo in Bot. Mag. Tokyo 56: 265 (1942) = Trigonotis chekiangensis (Migo) R. Mill, comb. nov. (tribe Trigonotideae)

O. chiangii Higgins in Phytologia 33: 412 (1976) = Mimophytum chiangii (Higgins) R. Mill (sect. 26.2)

O. controversa DC., Prodr. 10: 168 (1846) = O. nitida Hoffmans. & Link

O. cordata Hemsley in J. Linn. Soc. (Bot.) 26: 148 (1890) = Trigonotis moupinensis (Franch.) Johnston (tribe Trigonotideae)

O. cornifolia Lehm. in Ges. Nat. Freunde Berlin Mag. 8: 97 t. 2 (1818) = O. cappadocica (Willd.) DC.

O. cristata (Schreb.) Schrank in Denkschr. Akad. Wiss. München 3: 221 (1812) = Paracaryum cristatum (Schreb.) Boiss.

O. diffusa Maxim. in Bull. Acad. Pétersb. 27: 504 (1881) = Microula diffusa (Maxim.) Johnston (tribe Eritrichieae)

O. erecta Johnston in J. Arn. Arb. 16: 204 (1935) = Madrea erecta (Johnston) R. Mill (sect. 19.2)

O. esquirolii Lévl. in Feddes Rep. 12: 188 (1913) = Trigonotis cavalerei (Lévl.) Hand.-Mazz. (tribe Trigonotideae)

O. formosana Masamune in J. Soc. Trop. Agric. Taiwan 2: 240 (1930) = Trigonotis nankototaizanensis (Sasaki) Masamune & Ohwi ex Masamune (tribe Trigonotideae)

O. forrestii Diels in Notes R.B.G. Edinb. 5: 169 (1912) = Microula forrestii (Diels) Johnston (tribe Eritrichieae)

O. fortisii (Roemer & Schultes) G. Don, Gen. Syst. 4: 352 (1838) = ?

O. glochidiata (Decne.) Bunge in Mém. Sav. Étr. Pétersb. 7: 413 (1851) = Paracaryum intermedium (Fresen.) Lipsky

O. heterophylla Rech. fil. & H. Riedl in Öst. Bot. Zeitschr. 110: 513 (1963) = Lepechiniella heterophylla (Rech. fil. & H. Riedl) R. Mill, comb. nov. (tribe Eritrichieae)

O. hirsuta DC., Prodr. 10: 159 (1846) = Paracaryum hirsutum (DC.) Boiss.

O. howardii A. Gray in Proc. Amer. Acad. Arts Sci. 20: 262 (1885) = Eritrichium howardii (A. Gray) Rydberg (tribe Eritrichieae)

O. icumae Maxim. in Bull. Acad. Sci. Pétersb. 17: 452 (1872) = Trigonotis icumae (Maxim.) Makino (tribe Trigonotideae)

O. intermedia (Fresen.) Decne. in Ann. Sci. Nat. ser. 2, 2: 255 (1834) = Paracaryum intermedium (Fresen.) Lipsky

O. japonica (Thunb.) Maxim. in Bull. Acad. Sci. Pétersb. 17: 452 (1872) = Desmolopha japonica (Thunb.) R. Mill (sect. 25.2)

O. krameri Franch. & Savat., Enum. Pl. Japon. 1: 337 (1875) = Desmolopha krameri (Franch. & Savat.) R. Mill (sect. 25.2)

O. laevisperma Nakai in J. Jap. Bot. 23: 17 (1949) = Desmolopha krameri (Franch. & Savat.) R. Mill, var. laevisperma (Nakai) R. Mill (sect. 25.2)

O. lateriflora (Aubrey) Macbride in Proc. Amer. Acad. Arts Sci. 51: 543 (1916) = O. littoralis Lehm.

O. linophyllum St. Lag. in Ann. Soc. Bot. Lyon 7: 131 (1880) = O. linifolia (L.) Moench

O. longiflora (Bentham) DC., Prodr. 10: 158 (1846) = Lindelofia longiflora (Bentham) Baillon

O. lusitanica Schrank in Denkschr. Akad. Wiss. München 3: 221 (1812) = O. brassicifolia (Lag.) Lehm.

O. lusitanica (L.) Pourr., Herb. ex Lange, Pugill. 194 (1864) = O. nitida Hoffmans. & Link

O. mairei Lévl. in Feddes Rep. 12: 188 (1913) = Trigonotis mairei (Lévl.) Johnston (tribe Trigonotideae)

O. mexicana Watson in Proc. Amer. Acad. Arts Sci. 25: 158 (1890) = Mimophytum mexicanum (Watson) R. Mill, (sect. 26.2).

O. micrantha sensu Henderson & Hume, Lahore to Yarkand 328 (1873) non DC. (1846) = Paracaryum himalayense (Klotzsch & Garcke) C.B. Clarke

O. moupinensis Franch. in Nouv. Arch. Mus. Paris ser. 2, 10: 64 (1887) = Trigonotis moupinensis (Franch.) Johnston (tribe Trigonotideae)

O. myosotoides (Labill.) Schrank in Denkschr. Akad. Wiss. München 3: 222 (1812) = Paracaryum lithospermifolium (Lam.) Grande subsp. lithospermifolium

O. myosotoides sensu Fresen. in Mus. Senckenb. 1: 170 (1834) non (Labill.) Schrank (1812) = Paracaryum rugulosum (DC.) Boiss.

O. nana A. Gray in Proc. Amer. Acad. Arts Sci. 20: 262 (1885) = Eritrichium nanum (A. Gray) Greene (tribe Eritrichieae)

O. nervosa Edgeworth ex C.B. Clarke in Hooker fil., Fl. Brit. India 4: 158 (1883) = Paracynoglossum nervosum (Bentham ex C.B. Clarke) R. Mill (sect. 20.2)

O. olgae Brand in Feddes Rep. 26: 172 (1929 = Stephanocaryum olgae (Brand) M. Popov (tribe Eritrichieae)

O. omphalodes (L.) Voss in Vilm., Blumeng. ed. 3, 1: 693 (1896) nom. illeg. = O. verna Moench

O. papillosa DC., Prodr. 10: 159 (1846) = Paracaryum papillosum (DC.) Gürke

O. persica Boiss., Diagn. ser. 1(7): 30 (1846) = Paracaryum persicum (Boiss.) Boiss.

O. physodes Bunge in Mém. Sav. Étr. Pétersb. 7:/413 (1851) = Paracaryum physodes (Bunge) H. Riedl

O. pontica C. Koch in Linnaea 22: 646 (1848) = Paracaryum leptophyllum (DC.) Boiss.

O. prolifera Ohwi in Bull. Nat. Sci. Mus. Tokyo n.s. 3(no. 39): 98 (1956) = Desmolopha prolifera (Ohwi) R. Mill (sect. 25.2)

O. rugulosa DC., Prodr. 10: 160 (1846) = Paracaryum rugulosum (DC.) Boiss.

O. sempervirens (L.) D. Don, Prodr. Fl. Nepal 102 (1825) = Pentaglottis sempervirens (L.) Tausch ex L.H. Bailey (tribe Boragineae)

O. sericea Maxim. in Bull. Acad. Sci. St. Pétersb. 17: 453 (1872) = Trigonotis radicans (Turcz.) Steven (tribe Trigonotideae)

O. stricta C. Koch in Linnaea 17: 302 (1843) = Paracaryum strictum (C. Koch) Boiss.

O. thomsonii C.B. Clarke in Hooker fil., Fl. Brit. India 4: 161 (1883) = Paracynoglossum thomsonii (C.B. Clarke) R. Mill (sect. 20.2)

O. trichocarpa Maxim. in Bull. Acad. Sci. St. Pétersb. 25: 500 (1880) = Microula trichocarpa (Maxim.) Johnston (tribe Eritrichieae)

O. vaniotii Lévl. in Feddes Rep. 12: 188 (1913) = Trigonotis cavalerei (Lévl.) Hand.-Mazz. (tribe Trigonotideae)

O. verna Moench var. cachetica O. Kuntze in Acta Horti Petrop. 10: 218 (1887) = Anchusa myosotidiflora Lehm., teste Kusn.

24.2 SYSTEMATIC TREATMENT

Omphalodes (Tournefort ex) Miller, Gard. Dict. ed. 6 (Abridged ed. 3) (1754).

Syn: Picotia Roemer & Schultes, Syst. Veg. 4: 10 & 86 (1819) pro maxime parte; Omphalium Roth, Enum. Pl. Germ. 1: 590 (1827).

Lectotype (STAFLEU 1962): O. verna Moench. CZERAPANOV (1973) designated O. linifolia as type but this lectotypification is invalidated by the earlier one of Stafleu.

Perennial, biennial or annual, glabrous or villous herbs. Leaves alternate rarely opposite. Inflorescence a circinnate elongate cyme, bracteate or

ebracteate, or flowers solitary in leaf axils. Calyx divided to at least ½ and usually ± to base, ± accrescent in fruit, stellately spreading (rarely reflexed), undivided basal portion often also ± accrescent to form (usually very shallow) cup round nutlets. Corolla blue or white, often pink at first, subrotate to subcampanulate; tube short, usually not exceeding ½ length of limb; limb flat or concave, lobes ± patent. Faucal appendages (scales) trapeziform, papillose, ± emarginate at apex. Anthers included. Filaments very short, inserted below bases of scales. Style shorter than or rarely subequal to calyx. Gynophore rudimentary and flat, more rarely pyramidal. Nutlets 4, compressed, equalling or shorter than calyx lobes, oval, attached to gynobase by apex or by most of ventral surface, often pubescent, rarely minutely setulose; glochids always absent; disc usually smooth; wing present, either as a narrow callous rim or broader and incurving; margin of wing entire or dentate; areola oblong-lanceolate to orbicular, occupying 1/5-½ of ventral surface; embryo straight, very rarely curved (Su (Subgen. Maschalanthus).

1. Cauline leaves opposite (Subgen. Maschalanthus) ..... 14. scorpioides
1. Cauline leaves alternate (Subgen. Omphalodes)
  2. Gynobase pyramidal (Sect. Candollea)
    3. Wing of nutlets entire, erect
      4. Nutlets hairy ..... 12. littoralis
      4. Nutlets glabrous .....13. brassicifolia
    3. Wing of nutlets strongly incurved, crenate or dentate
      5. Inflorescence bracteate; flowers blue ..... 9. kusinskyanae
      5. Inflorescence ebracteate; flowers white
        6. Margin of nutlets incurved, obtusely dentate and transversely rugose ..... 10. linifolia
        6. Margin of nutlets erect, ciliate-dentate .....11. pavoniana
  2. Gynobase ± flat and rudimentary (Sect. Omphalodes)

7. Rhizomes creeping, stoloniferous (Subsect. Omphalodes) ..... 6. verna

7. Rhizome (if present) not stoloniferous

8. Leaves with patelliform tubercles and often glaucous (Subsect. Lucilianthe)

9. Calyx hardly accrescent (to 6 mm) in fruit; flowers normally blue; nutlets with entire margin ..... 7. luciliae

9. Calyx greatly accrescent (to 13 mm) in fruit; corolla always milk-white; nutlets with fimbriate margin 8. ripleyana

8. Leaves lacking tubercles and never glaucous

10. Lateral veins of leaves ± parallel; inflorescence ebracteate (Subsect. Nitidae) ..... 5. nitida

10. Lateral veins of leaves ± arcuate; inflorescence usually bracteate (Subsect. Caucasicae)

11. Leaves deeply cordate at base, with very distinct veins ..... 4. cappadocica

11. Leaves shortly cuneate, truncate or rarely obscurely cordate at base, with rather indistinct veins

12. Corolla white ..... 3. kusnetzovii

12. Corolla blue

13. Corolla 10-15 mm diam.; margin of nutlets indistinctly dentate ..... 2. rupestris

13. Corolla 20 mm diam.; margin of nutlets strongly dentate ..... 1. lojkae

Subgen. Omphalodes

Perennials or annuals. Lower cauline leaves always alternate, glabrous or with simple trichomes or patelliform tubercles, hairs never arising from bulbous bases surrounded by calcareous subsidiary cells. Inflorescence racemose, bracteate in lower part or ebracteate. Embryo straight, radicle very short.

Sect. Omphalodes. Syn: Omphalodes sect. Euomphalodes A. DC. in DC., Prodr.

10: 161 (1846) nom. illegit.; O. sect. Arctotertiariae M. Popov in Fl. URSS 19: 609 (1953) nom. invalidum.

Perennials. Rhizome ± thick, very rarely bearing stolons. Stems and leaves usually green, rarely glaucous. Corolla most often blue, rarely white. Gynobase rudimentary, flat or shortly pyramidal. Nutlets small, c. ½ x accrescent calyx, attached to gynobase by ± whole of ventral surface, pilose (hairs never hooked) or glabrous.

- - Subsect. Caucasicae R. Mill, subsect. nov.

Herbae perennes numquam glaucae, rhizomatibus subhorizontalibus, radices pernumerosas tenuissimas emittentibus. Folia ± coriacea, apice acuminata vel mucronata, base cordata usque ad attenuata, venis ± arcuatis, ± prominenter elevatis. Inflorescentia saepius in parte inferiore bracteata. Gynobasis rudimentalis, plana vel plano-pyramidata. Nuculae dense vel sparse pubescentes, numquam glabrae, margine semper ± dentato.

Perennial herbs with subhorizontal rhizomes producing numerous very slender adventitious roots. Leaves ± coriaceous, apex acuminate to mucronate, base attenuate to cordate, veins arcuate, ± elevated on lower surface of lamina. Inflorescence usually bracteate in lower part. Gynobase rudimentary, flat or flat-pyramidal. Nutlets densely or sparingly pubescent (never glabrous), margin ± dentate and incurving.

Type: O. lojkae Somm. & Lev. in Acta Horti Petrop. 12: 157 (1892).

1. O. lojkae Somm. & Lev., loc. cit. (1892).

2. O. rupestris Rupr. in Boiss., Fl. Or. 4: 267 (1875).

3. O. kusnetzovii Kolak. in Zam. Sist. Geogr. Rast. Tiflis 14: 62 (1948).

4. O. cappadocica (Willd.) DC., Prodr. 10: 161 (1846).

- - Subsect. Nitidae R. Mill, subsect. nov.

Herbae perennes, numquam glaucae, rhizomate non stolonifero. Folia superne viridia nitida glabra, subtus griseo-pubescentia, sine tuberculis; basalia longissima, obovata, distincte triplinervia; veni laterales prope marginem paralleles non elevati, ad costam venulis indistinctis conducti. Inflorescentia ebracteata terminalis. Gynobasis rudimentalis, plana.

Nuculae parvae margine incurvato. - Species unica.

Perennials, erect, not stoloniferous. Leaves glabrous, shining green above, grey-pubescent below, tubercles absent; basal ones very long, obovate, attenuate, distinctly 3-nerved, lateral veins near margin, parallel to midrib and linked to the latter by indistinct veinlets. Inflorescence ebracteate, terminal. Gynobase rudimentary, flat. Nutlets small, margin incurved. - Monotypic.

Type: 5. O. nitida Hoffmans. & Link, Fl. Port. 1: 194, t. 25 (1809).
(= O. lusitanica auct.)

- - Subsect. Omphalodes

Perennials, never glaucous. Rhizomes creeping, stoloniferous. Leaves sericeous-villous, soon glabrescent, tubercles absent; veins arcuate with distinct reticulate network of veinlets; lateral veins not prominently raised on lower surface. Inflorescence ebracteate, terminal. Gynobase rudimentary. Nutlets with simple straight hairs and entire, callous margin. - Monotypic.

6. O. verna Moench, Meth. 420 (1794).

- - Subsect. Lucilianthe R. Mill, subsect. nov.

Herbae saxatiles rhizomatibus crassis lignosis. Folia elliptica usque ad orbicularia, saepius glauca vel glaucescentia, rariore viridia, superne subtusque glabra sed tuberculis patelliformibus esetulosis saepe calcaratis obsita, venis pinnatis indistinctis non elevatis. Inflorescentia in parte inferiore bracteata. Gynobasis breviter pyramidata, nuculae glabrae vel sparse pilosae, margine calloso incurvo, dentato vel integerrimo.

Saxatile herbs with thick woody rhizomes. Leaves elliptic to orbicular, usually glaucous to glaucescent, more rarely green, glabrous on both surfaces but with saucer-shaped tubercles not bearing setules; venation pinnate, indistinct, veins not raised. Inflorescence bracteate in lower part. Gynobase shortly pyramidal, nutlets glabrous or sparsely pilose, wing callous and incurved, with entire or dentate margin.

Type: O. luciliae Boiss., Diagn. ser. 1(4): 41 (1844).

7. O. luciliae Boiss., loc. cit. (1844).

8. O. ripleyana Davis in Notes R.B.G. Edinb. 22: 82 (1956).

Sect. Candollea R. Mill, sect. nov. Syn: Omphalodes sect. Paracaryum DC. grex 2 calyx accrescentes nuculis maturis longior aut eas subaequans A. DC. in DC., Prodr. 10: 160 (1846); O. sect. Pseudoparacaryum M. Popov in Fl. URSS 19: 616 (1953) nom. illegit.

Herbae annuae saepissime glaucae, radicibus tenuibus sine rhizomate. Folia glaberrima, tuberculis patelliformibus calcaratis setuliferis excepta. Corolla alba, rariore pallide caerulea vel albido-caerulea. Gynobasis bene evoluta, pyramidata. Nuculae maiores quam eos sectionis Omphalodis, calycem subaequantes, ad apicem gynobasi areola magna affixae, glabrae vel setulis semper barbatis obsitae. - Hic sectio novus in honorem botanici celeberrimi florae mundi investigatoris clarissimi Alphonse De Candolle nominatus est.

Annual herbs with slender tap roots, never stoloniferous, lacking rhizomes. Plants usually glaucous. Leaves glabrous except for calcareous tubercles bearing minute setules. Corolla white, more rarely pale blue or bluish-white. Gynobase pyramidal. Nutlets larger than in sect. Omphalodes, subequalling calyx, glabrous or with (always hooked) setules.

Type: O. linifolia (L.) Moench, Meth. 419 (1794).

9. O. kusinskyanae Willk. in Öst. Bot. Zeitschr. 39: 318 (1889).

10. O. linifolia (L.) Moench, loc. cit. (1794).

11. O. pavoniana Boiss., Diagn. ser. 1(11): 128 (1849).

12. O. littoralis Lehm. in Ges. Nat. Freunde Berlin Mag. 8: 98 (1818).

13. O. brassicifolia (Lag.) Lehm., Asperif. 185 (1818).

subgen. Maschalanthus (DC.) R. Mill, stat. nov. Syn: Omphalodes Miller sect. Maschalanthus DC., Prodr. 10: 161 (1846).

Biennial or annual decumbent herb. Cauline leaves opposite, but alternate in flowering region; trichomes arising from bulbous bases

impressed into surface of lamina and surrounded by ± calcareous subsidiary cells. Flowers solitary, axillary, small. Gynobase minute, greatly reduced. Nutlets attached to gynobase by small circular areola, pilose-pubescent, hairs not hooked. Embryo curved, radicle adpressed to and equalling cotyledons. - Monotypic.

Type: 14. O. scorpioides (Haenke) Schrank in Denkschr. Akad. Wiss. München 3: 222 (1812).

24.3 MORPHOLOGY

The distinctive morphological features of the taxonomic groups recognised above will now be discussed.

24.3.1 Rootstock:

The two subgenera recognised differ widely in the form of the rootstock, and similar but less marked differences are shown by the members of the different ranks within subgen. Omphalodes. The perennial habit would appear to be the least specialised condition, and the annual habit has arisen at least twice.

Sect. Omphalodes is characterised by perennial rhizomatous rootstocks. O. lojkae, O. kusnetzovii and O. rupestris (subsect. Caucasicae), which inhabit stony alpine taluses and boulder country in Caucasia where the soil is undoubtedly quite shallow, have short rootstocks which develop a mass of slender adventitious roots. In the remaining species of O. subgen. Omphalodes sect. Omphalodes there is a tendency towards development of the rootstock and the suppression of long adventitious roots, and for the rootstock to become more horizontal, longer and thinner. O. cappadocica (subsect. Caucasicae) has a fairly slender, often elongating subhorizontal flexuous rootstock, which still produces numerous adventitious roots. In O. nitida (subsect. Nitidae) the rather short rhizome produces few roots, while in O. verna (subsect. Omphalodes) the long creeping stoloniferous rhizome is slender and produces short adventitious rootlets mainly at the nodes.

The saxicolous chasmophytes of subsect. Lucilianthe (O. luciliae and O. ripleyana) on the other hand are adapted to their environment by the development of stout, tapering erect rhizomes which are clothed with old leaf bases and which appear to produce few rootlets. This development is analogous to that found in chasmophytes belonging to other genera of Boraginaceae occurring in the same area (Lycian Taurus, Turkey), e.g. Paracaryum lithospermifolium.

Sect. Candollea is characterised by annual habit. The rhizome is wholly suppressed and is replaced by a long slender erect tapering tap root producing few short secondary roots - probably an adaptation to the sandy xeric habitats in which these Lusitanian species occur.

O. scorpioides (subgen. Maschalanthus) is a mesophytic species of the forests of C. & E. Europe and is also annual or biennial. However, it differs from the species of sect. Candollea in having numerous, weak and slender roots.

24.3.2 Stems:

With respect to the stem, the principal tendencies shown by the genus are:

1. reduction in the number of stems arising from the rootstock;
2. development of trailing habit;
3. glabrescence.

In the rupestral species of subsects. Caucasicae and Lucilianthe numerous erect to ascending stems arise from the crown. In subsect. Caucasicae the stems normally have adpressed hairs, although glabrescent forms may rarely occur. The members of subsect. Lucilianthe are glabrous and show glaucous tendencies. O. nitida (subsect. Nitidae) has a solitary, erect glabrous stem, while in O. verna (subsect. Omphalodes) the stems are also glabrous, and semi-trailing in habit.

Branching is not common in the vegetative portions of the stem in subgen. Omphalodes, although in some species the inflorescence may be branched.

In sect. Candollea, robust forms of O. linifolia and O. brassicifolia may branch in the upper part giving a paniculate inflorescence, while the branched habit is further developed in some forms of O. littoralis. All these three species tend to be glaucous, and stem hairs are absent or confined to the upper part of the inflorescence, where sparse adpressed setules normally develop and become denser on the pedicels. In contrast, O. scorpioides of subgen. Maschalanthus has weak decumbent strongly branching stems bearing short adpressed setules throughout.

24.3.3 Leaves:

a) Development:

Differentiation into radical and cauline leaves is a feature of the perennial species of subgen. Omphalodes. The radical leaves are always long-petiolate and develop on germination, which may be autumnal or vernal. In subsects. Caucasicae and Lucilianthe they develop in autumn and overwinter, being adapted to the severe Caucasian and Anatolian winters by a ± coriaceous epidermis and, in subsect. Caucasicae, an indumentum of downy hairs. In O. nitida and O. verna, however, they appear not to develop until the spring and enlarge during the flowering season; especially in O. verna, their texture tends to be thinner and more membranous. POPOV (1953) in this respect was incorrect in including O. cappadocica in the same series (ser. Vernales M. Popov) as O. nitida and O. verna; although there are similarities in some leaf characters between O. verna and O. cappadocica, the latter species seems more closely allied in its leaf morphology to the other three Caucasian species, which Popov placed in ser. Rupestres.

Among the annual species, radical leaves develop in O. scorpioides (subgen. Maschalanthus) but are apparently not found in subgen. Omphalodes sect. Candollea. In O. scorpioides the radical leaves, which are rarely mentioned in modern descriptions, are quite distinct from the lower

cauline leaves, being small but broadly elliptic; they seem to develop in spring.

Well-developed cauline leaves are always present in Omphalodes, and are all normally alternate. O. scorpioides is unique in the genus in having almost all cauline leaves opposite, at least in the non-flowering portion. In this respect it parallels the totally unrelated species Rindera neubaueri from Afghanistan, which, like O. scorpioides, is also anomalous in its genus in other respects (see sect. 9.3) and is also placed in a monotypic infrageneric category.

The species of Omphalodes show a gradual tendency for the cauline leaves to become sessile. Long-petiolate leaves occur in O. verna but the development of the petiole is here probably secondary, as the species is advanced both in other morphological characters and palynologically. O. lojkae and other species of subsect. Caucasicae have cauline leaves short-petiolate only in the lower part of the stem, as in subsect. Lucilianthe. In sect. Candollea all leaves are sessile, and in O. brassicifolia they tend to be amplexicaul.

b) Leaf Shape:

In subsect. Caucasicae the leaves are ± elliptic, with acuminate or mucronate apex. From O. lojkae to O. cappadocica there is a tendency towards a more ovate outline with cordate base. Elliptic leaves also occur in subsect. Lucilianthe (tending towards orbicular), while O. verna parallels O. cappadocica in its ovate, cordate radical leaves although these are much smaller than those of the latter. O. nitida has very long, narrowly elliptic leaves, equalling or exceeding 15 cm, with very attenuate base.

c) Indumentum:

Trends in leaf indumentum closely follow those outlined above for the stem (sect. 24.3.2). O. scorpioides (subgen. Maschalanthus) has the leaves finely adpressed-setulose (Fig. 24.1, no. 10a, b). The setules arise

from bulbous unicellular bases impressed in to the epidermides and surrounded by a single ring of subsidiary cells which may become white and calcified with age. O. scorpioides is the only member of Omphalodes to have this type of trichome base, which elsewhere in the Cynoglosseae is frequent in Paracaryum, Cynoglossum, etc.

In subgen. Omphalodes, indumentum types are diverse but with a tendency towards glabrescence, frequently associated with glaucescence. Strigillose hairs occur densely on both surfaces of the lamina of sect. Omphalodes subsect. Caucasicae (Fig. 24.1, nos. 1a, 2a, 2b), and more sparsely in O. verna (ic. cit. nos. 3a, 3b). O. nitida (ic. cit. nos. 4a, 4b) is unique in the genus in having discolorous leaves, dark green, shining and quite glabrous above, with dense short grey hairs below. Glabrescent leaves occur in sect. Candollea (ic. cit. nos. 7, 8, 9a, b) and in sect. Omphalodes subsect. Lucilianthe (ic. cit. nos. 5a, b, 6a, b). In both these taxa, which inhabit dry calcareous habitats, there has been development of flattish, slightly elevated saucer-shaped tubercles, both on the leaf lamina and, in some species, also on the calyx lobes. These patelliform tubercles morphologically resemble those found in some species of Rindera and Trachelanthus. In all the species of sect. Candollea they always possess a central, very short, obtuse setule (as in Rindera), but in subsect. Lucilianthe the tubercles always lack such setules and there is no evidence that they have become detached. In all five species, the presence of tubercles is a constant character, as is their total absence in members of any other subsection. In O. luciliae (ic. cit. nos. 5a, b), however, they tend to be inconspicuous and hyaline-transparent, especially in subsp. scopulorum Edmondson and on the current year's cauline leaves of the other three subspecies. On older leaves they normally become calcified and greenish-white.

d) Venation:

The venation of the lamina has been found to be a useful differential

character, especially at subsectional level. The lamina of radical and cauline leaves possess similar venation but since the character is easier to observe in the radical leaves these were used as the basis for the following observations.

POPOV (1953) appears to have been the earliest author to note correlations between venation type and other morphological characters, and he used them in his sectional and series descriptions. However, he stressed not so much the pattern of venation but rather the degree of elevation of the veins on the lower surface. Possibly on account of inadequate representation of European species, he erroneously stated that O. cappadocica, O. nitida and O. verna share the characters of 'markedly protruding pinnately lateral nerves'. In fact, of these species, only O. cappadocica has this combination of characters; the other two species have the veins very indistinctly elevated or not at all. His other series, ser. Rupestres, was said to be characterised by 'indistinctly protruding lateral nerves' - a fact which has been confirmed by observation of material of O. lojkae. In order that O. cappadocica might be accommodated, I have amended the description to 'lateral veins ± distinctly protruding', to contrast with the remaining subsections ('lateral veins not or indistinctly protruding').

The venation pattern is here considered to be of more importance. Four patterns can be recognised within sect. Omphalodes (Fig. 24.1, nos. 1-10); terminology follows HICKEY & WOLFE (1976):

1. (Subsect. Caucasicae): radical leaves with antrorsely arcuate, pinnately lateral, brochidodromous veins. In O. lojkae (no. 1), the 5-6 pairs of veins are slightly raised above the lower surface of the lamina, and curve upwards towards the margin but without touching it, successive veins fusing with the one above very near the leaf margin and near their terminations. From POPOV's illustrations (Fl. URSS 19: t. 32, f. 2, 1953) it would appear that similar venation is found in O. rupestris. O. cappadocica (no. 2) differs by its very prominent elevated veins, of which the lowest 2-3 pairs

Figure 24.1

Omphalodes: Leaf Morphology

1 O. lojkae, x 0.45 (Marcowicz 215) 1a indumentum, x 35 (both surfaces similar)

2 O. cappadocica, x 0.45 (Rix 2020) 2a upper surface indumentum, x 35; 2b lower surface indumentum, x 35

3 O. verna, x 0.45 (Baron Rastern in Herb. Dörfler) 3a upper surface, x 35; 3b lower surface, x 35

4 O. nitida, x 0.45 (Sinclair 4630) 4a upper surface, x 35; 4b lower surface, x 35

5 O. luciliae, x 0.87 (Archibald 3008) 5a upper surface, x 35; 5b lower surface, x 35

6 O. ripleyana, x 0.87 (Davis 15680) 6a upper surface, x 35; 6b lower surface, x 35

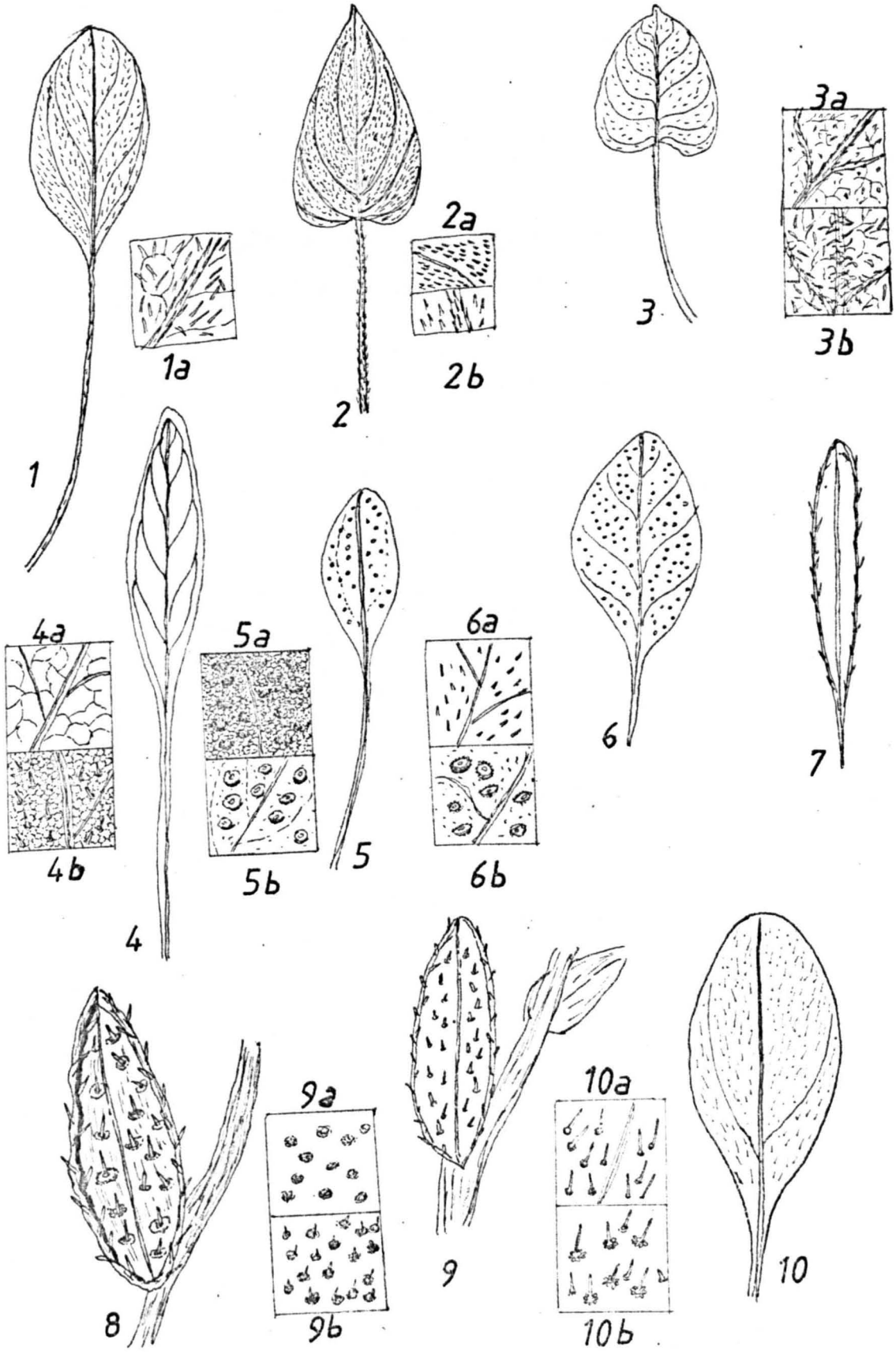
7 O. linifolia, x 0.87 (Ritzberg 26 vii 1888)

8 O. littoralis, x 5.25 (Delalande 27 v 1850)

9 O. brassicifolia, x 1.75 (Reverchon 448) 9a upper surface, x 35; 9b lower surface, x 35

10 O. scorpioides, x 1.75 (Barth 20 iv 1899) 10a upper surface, x 35; 10b lower surface, x 35

Figure 24,1



arise from almost the same point on the midrib, just above the cordate base of the lamina. Lateral veins then curve outwards to near the margin of the lamina, then inwards, to fuse with the next successive vein at a point well below its termination.

2. (Subsect. Omphalodes): In O. verna (no. 3), the venation pattern is similar to that of O. cappadocica but the number of vein-pairs (c. 9) is almost twice that of the latter species. Reticulate veinlets connecting the indistinct laterals are usually conspicuous.

3. (Subsect. Nitidae): O. nitida (no. 4) has a particularly distinctive venation pattern which is closely paralleled in Cynoglossum and related genera. There are two principal lateral veins which run continuously from base to apex, parallel to and just within the leaf margin, and which are linked to the midrib by distant, slightly arcuate veinlets.

4. (Subsect. Lucilianthe): the species of this subsection are closest in venation pattern to that of O. lojkae but differs in their straight, not arcuate veins. In O. luciliae (no. 5) the venation is especially indistinct (almost invisible) but the pattern is evident in O. ripleyana (no. 6).

In O. littoralis (no. 8), O. brassicifolia (no. 9) and O. linifolia (no. 7) of sect. Candollea and O. scorpioides (no. 10) of subgen. Maschalanthus, the venation is so indistinct, apart from the midrib, as to be invisible on mounted herbarium material.

24.3.4 Inflorescence:

The inflorescence may be differentiated or not; if differentiated, the cymes may be bracteate or ebracteate. The differentiated bracteate condition would appear to be normally the least specialised, being found in species of sect. Candollea (e.g. O. littoralis) and sect. Omphalodes subsect. Caucasicae (e.g. O. lojkae, O. rupestris). O. cappadocica and O. verna may have the extreme base of the inflorescence bracteate or not, while ebracteate cymes occur in O. nitida (subsect. Nitidae) and also in

O. linifolia and O. brassicifolia (sect. Candollea). If differentiated, the inflorescence is normally single, unbranched and racemose, but may be branched, appearing paniculate, in O. linifolia and O. brassicifolia. The species of subsect. Lucilianthe show a transition toward the undifferentiated state. The main part of the inflorescence is bracteate near the base, and below it there are usually 1 or more isolated subterminal axillary flowers on longer pedicels. In O. scorpioides the inflorescence is completely undifferentiated; the small flowers are solitary in the leaf axils and borne on long capillary pedicels.

24.3.5 Pedicels:

In all species of the genus the flowers are borne on long pedicels exceeding the calyx and elongating in fruit. The thickness of the pedicels varies from capillary in O. scorpioides to moderately stout in sect. Candollea. In all taxa except sect. Candollea (where the pedicels remain stiff and erecto-patent at maturity) there is a ± strong tendency for the pedicels to become deflexed or even hamately drooping in fruit.

The indumentum of the pedicels bears a close resemblance to that of the stem (if any), but the density of trichomes tends to be greater. In some glabrous-stemmed species, e.g. O. linifolia, sparse adpressed trichomes similar to those of the calyx may be present on the pedicels, but in subsect. Lucilianthe they are glabrous.

24.3.6 Calyx:

In both subgenera the calyx is ± regularly 5-lobed to near the base and is ± accrescent in fruit; accrescence is particularly marked in subsect. Lucilianthe. An apparently unique feature of O. ripleyana of that subsection is the greatly accrescent calyx in which both upgrowth of the undivided basal portion to form a short calyx tube in which the nutlets mature, and outgrowth of the lobes, occur. The lobes become stellately spreading, brown and papyraceous (Fig. 24.3, no. 4a). O. luciliae shows similar but much less

marked accrescence and the calyx apparently remains green (ic. cit. no. 3).

The calyx is hairy in most taxa, including those with glabrous leaves and stems, but is glabrous (except for tubercles) in subsect. Lucilianthe.

24.3.7 Corolla (Figure 24.2):

The corolla varies from subrotate to almost campanulate. The subrotate condition prevails in both sections of subgen. Omphalodes. Evidence from comparative study of immature and mature flowers of O. lojkae suggests that the hypocrateriform corolla arises as a result of differential rates of growth of tube (slower) and limb, since the tube is relatively longer in immature corollas than in those at anthesis. In subgen. Maschalanthus the tube remains relatively long and may be subequal to the limb, thus resulting in a subcampanulate corolla with distinct patent limb. The limb is lobed to at least halfway in most species of subgen. Omphalodes but may be lobed nearly to the base, as in sect. Candollea and in subgen. Maschalanthus. In most cases, the lobes are rounded, broad and obtuse with relatively narrow sinuses (which are not plicate) between them. Subgen. Maschalanthus is characterised by its more elliptic, narrower lobes, while in sect. Candollea most species have large rounded sinuses between the lobes.

The corolla at anthesis is normally either blue or white. In some blue-flowered species the buds are pink, e.g. O. luciliae; a collection of O. luciliae (Darrah 64!) has been reported as having red flowers, but the collector did not state whether this observation referred to buds or fully-open flowers.

Most blue-flowered species rarely produce white variants, which in some cases (e.g. O. verna) have been introduced to horticulture. Rarely, the normally white-flowered species O. linifolia (Fig. 24.4) will produce corollas whose lobes become pale bluish with age (cf. Smythies 79!).

Notwithstanding these sporadic variants, the normal colour of the corolla is a useful taxonomic character at all levels. The colour when fresh and dry, and that of a boiled-up corolla, are indicated in Table 24.1.

Table 24.1

Colour of fresh and boiled-up corollas of species belonging to different infrageneric taxa within Omphalodes

Taxon	Colour fresh	Colour dry	Colour after boiling
Subgen. Maschalanthus	pale blue	pale blue-grey	whitish
Subgen. Omphalodes:			
Sect. Candollea	white in species examined	white (sometimes with blue tinge) in species examined	yellowish-white to deep lemon yellow
Sect. Omphalodes			
Subsect. Caucasicae	sky blue	grey-blue	grey-blue to brown-blue
Subsect. Omphalodes	bright blue	bright blue	bright blue
Subsect. Nitidae	deep blue	deep blue	deep blue
Subsect. Lucilianthe	bright blue or white	bright blue or white	bright blue or white

Exceptions to Table 24.1 include O. kusinskyanae, here included in sect. Candollea because of its reported relationship with O. linifolia (BRAND 1921; TUTIN et al. 1972), which has blue corollas; and O. kusnetzovii which is included in subsect. Caucasicae following Popov's inclusion of it in the same series as O. lojkae and O. rupestris, but which has white corollas. I have seen material of neither species.

Reference to the table shows that in some taxa the colour is ± permanent, while in others some quite marked colour changes occur on drying and especially on boiling of a previously dried corolla. The evidence suggests that the chemical composition of the pigments involved may be different in the various taxonomic groups but no research on this subject seems to have been reported. The bright yellow colour of the boiled corolla of sect.

Figure 24.2

Omphalodes: Corolla Morphology

(All drawings are of opened-out corollas, x 4.4)

1 O. lojkae (Desoulavy 16 vi 1899)

2 O. cappadocica (Tobey 1512)

3 O. nitida (Sinclair 4630)

4 O. verna (Davis 34050)

5 O. luciliae (Parry 1)

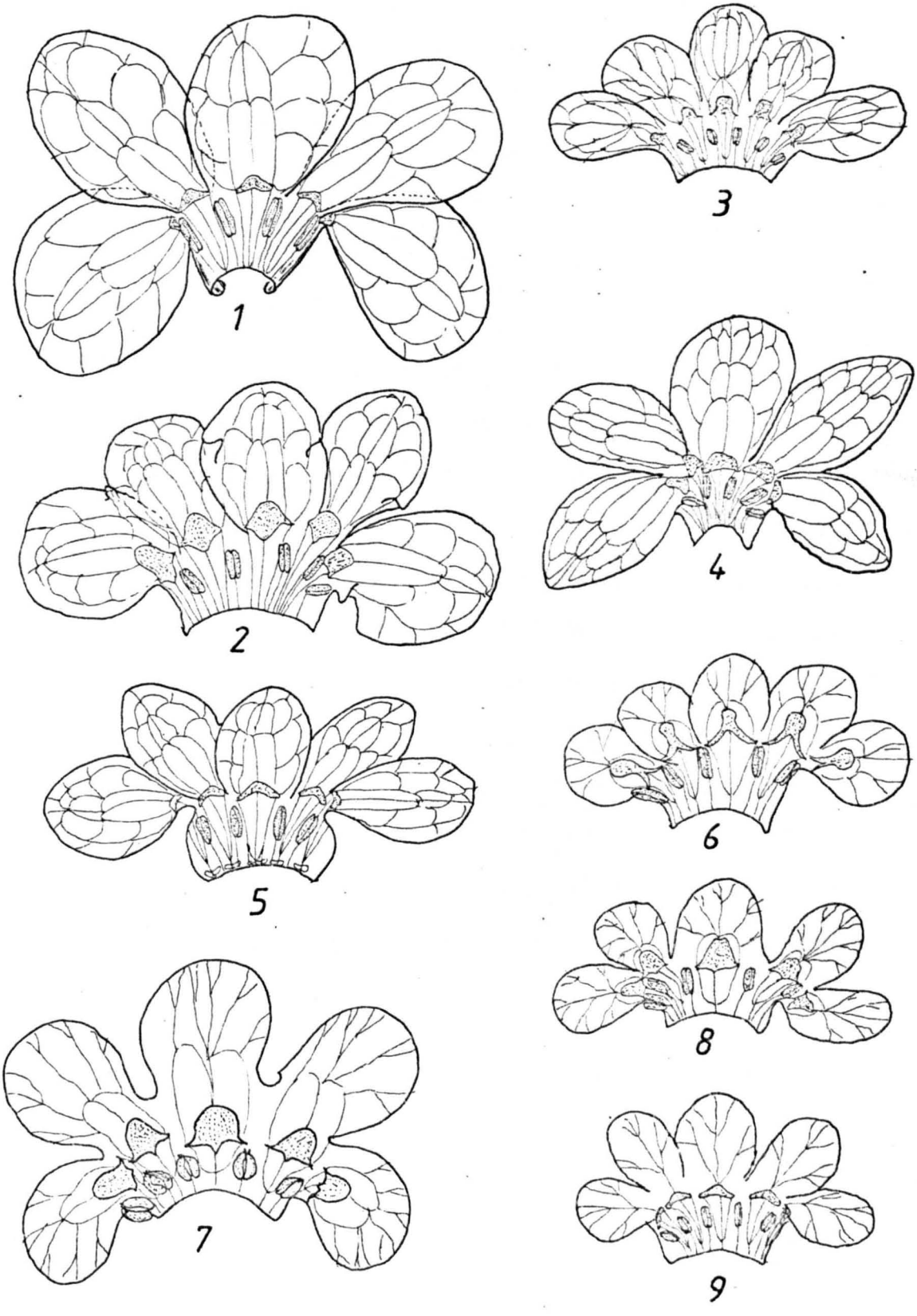
6 O. linifolia (Smythies 79)

7 O. brassicifolia (Stocken 351.64)

8 O. littoralis (Delalande s.n.)

9 O. scorpioides (Nos 2364)

Figure 24,2



Candollea, but not in other white-flowered taxa, suggests that the pigments of O. linifolia and its allies are different from the other white-flowered taxa.

Within subgen. Omphalodes, corolla colour and gynobase characters are strongly correlated at the sectional level. The contrast is between sect. Omphalodes (corollas predominantly blue; nutlets attached by ventral surface to rudimentary ± flat gynobase) and sect. Candollea (corollas predominantly white; nutlets attached by large subapical areola to well-developed pyramidal gynobase). Gynobase characters are discussed in greater detail below (sect. 24.3.8).

Faucal scales are present in all species of Omphalodes. In subgen. Omphalodes they tend to be trapeziform or broader than long, while they are reduced to broad semi-lunar folds with produced apex in subgen. Maschalanthus. In sect. Candollea of subgen. Omphalodes, they are normally triangular and longer than broad. In all species examined, the apex of the scales is ± emarginate and papillose.

The scales are concolorous with the corolla limb in subgen. Omphalodes sect. Candollea (white in those examined). In most species of subgen. Omphalodes sect. Omphalodes, however, they are discolorous, being white in subsect. Caucasicae and in O. luciliae (subsect. Lucilianthe) but yellow in O. nitida and O. verna.

Small squarish annular scales, notched both at apex and base, are well developed at the base of the corolla tube in O. luciliae (Fig. 24.2, no. 5). They have not been observed in any other species. They may be expected to occur in the related O. ripleyana but in the two specimens seen, the single flower is on the holotype and unavailable for dissection.

The anthers in all species are elliptic to ovoid, medifixed on very short filaments, and inserted in the corolla tube so that the anther apices are level with or below the scale bases. Their colour varies from dark grey to black in sect. Candollea, through brown in sect. Omphalodes

subsects. Caucasicae and Nitidae, to yellowish in O. luciliae and O. verna. O. scorpioides (subgen. Maschalanthus) has dark brown anthers.

24.3.8 Nutlets (Figure 24.3):

All four nutlets usually mature. In subgen. Maschalanthus and in some species of subgen. Omphalodes, the gynobase is hardly developed, being very small, flat and rudimentary. In most members of subgen. Omphalodes, the nutlets are attached to the flat gynobase by a large part of their ventral surface and, on account of their mainly lateral (not ventral) growth, they form a flat cross on the calyx. In O. scorpioides, however, they are attached to the gynobase only by a small roundish scar. In subsect. Lucilianthe, the gynobase is slightly convex, but in their nutlet attachment these two species resemble the others of sect. Omphalodes.

The members of sect. Candollea are unique in the genus in the considerable development of the gynobase, which in these species is elevated and high-pyramidal, resembling that of Paracaryum. Also as in Paracaryum, the nutlets form a pyramid but they are attached to the gynobase by a nearly apical, lanceolate scar. The similarities to Paracaryum influenced De Candolle, who classified these species as a special group in his sect. Paracaryum, and they were doubtless also in Popov's mind when he selected the (invalid) name Pseudoparacaryum for the section. However, on account of the otherwise considerable differences between Paracaryum as here delimited and these Omphalodes species, I have chosen not to validate Popov's rather misleading name, but rather to name the section in honour of De Candolle who was the earliest author to note the similarity between the (then) three recognised species and award them special taxonomic rank.

In all species except those belonging to sect. Candollea, the nutlets are much shorter than the ± patent fruiting calyx lobes. In sect. Candollea, however, the nutlets equal or slightly exceed the calyx, which becomes somewhat deflexed in fruit, in the same manner as Paracaryum but less marked.

Figure 24.3

Omphalodes: Nutlet Morphology

1 O. verna: nutlet and calyx, x 4.4 (Davis 34650)

2 O. cappadocica (Rix 2020): 2a nutlets and calyx, x 4.4
2b nutlet, dorsal view, x 8.7

3 O. luciliae: nutlets and calyx, x 8.7 (Findlay 118)

4 O. ripleyana (Davis 15680): 4a nutlets and calyx, x 4.4
4b nutlet x 17.5

5 O. nitida, dorsal view of nutlet, x 8.7 (Sinclair 4630)

6 O. linifolia: group of nutlets, x 8.7 (Pedro da Campo in Herb. Bourgeau 67)

7 O. littoralis: nutlets and calyx, x 8.7 (Delalande 27 v 1850)

8 O. brassicifolia: dorsal and dorso-lateral views of nutlets, x 8.7 (Reverchon 448)

9 O. scorpioides: nutlets and calyx, x 8.7 (Tauscher 1872)

Figure 24,3

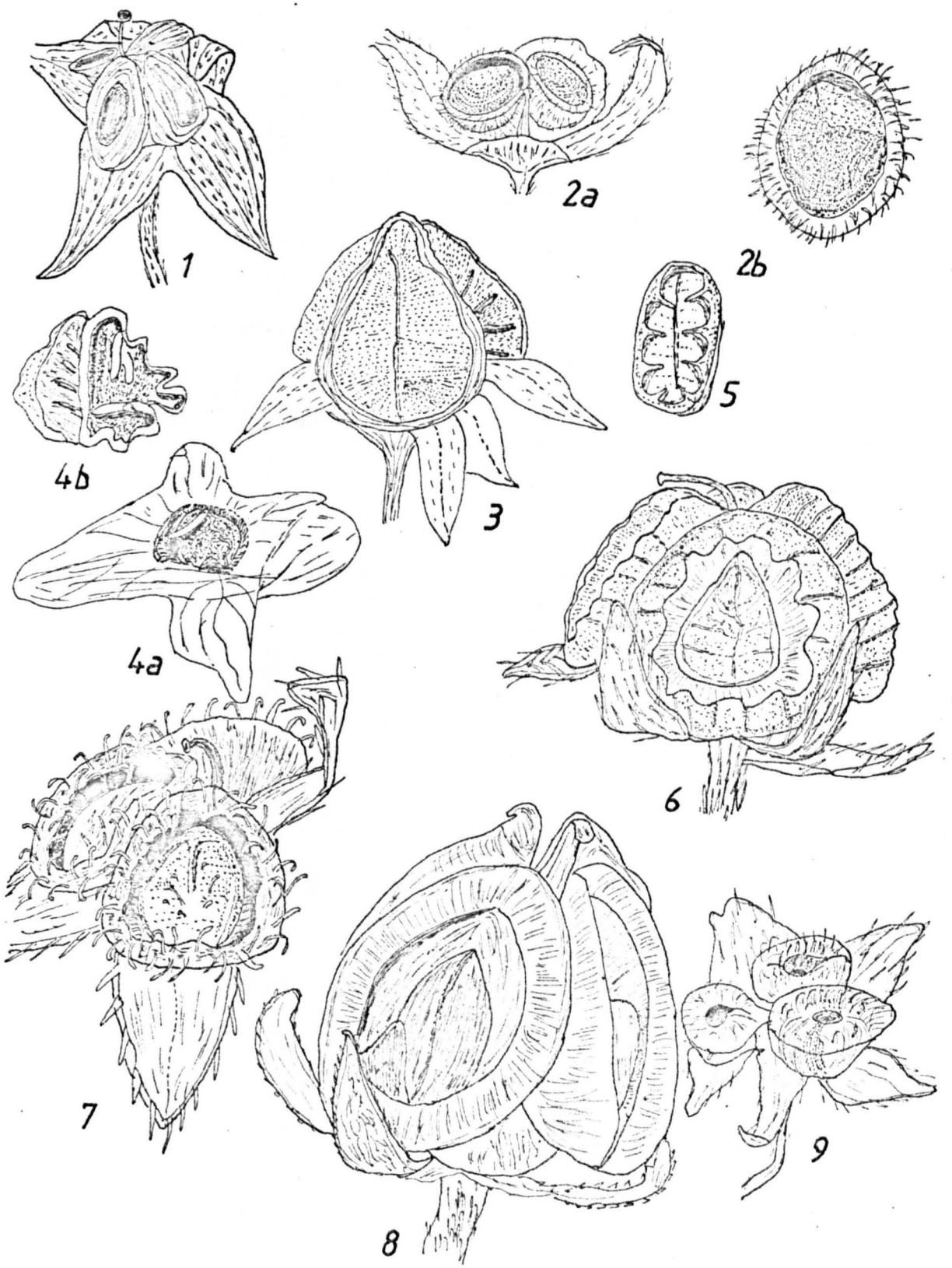


Figure 24.4

Omphalodes linifolia (Spain, prov. Malaga, Pena de Los Enamorados, 500 m, 27 April 1977, R.R. Mill 1865 (hb. E)

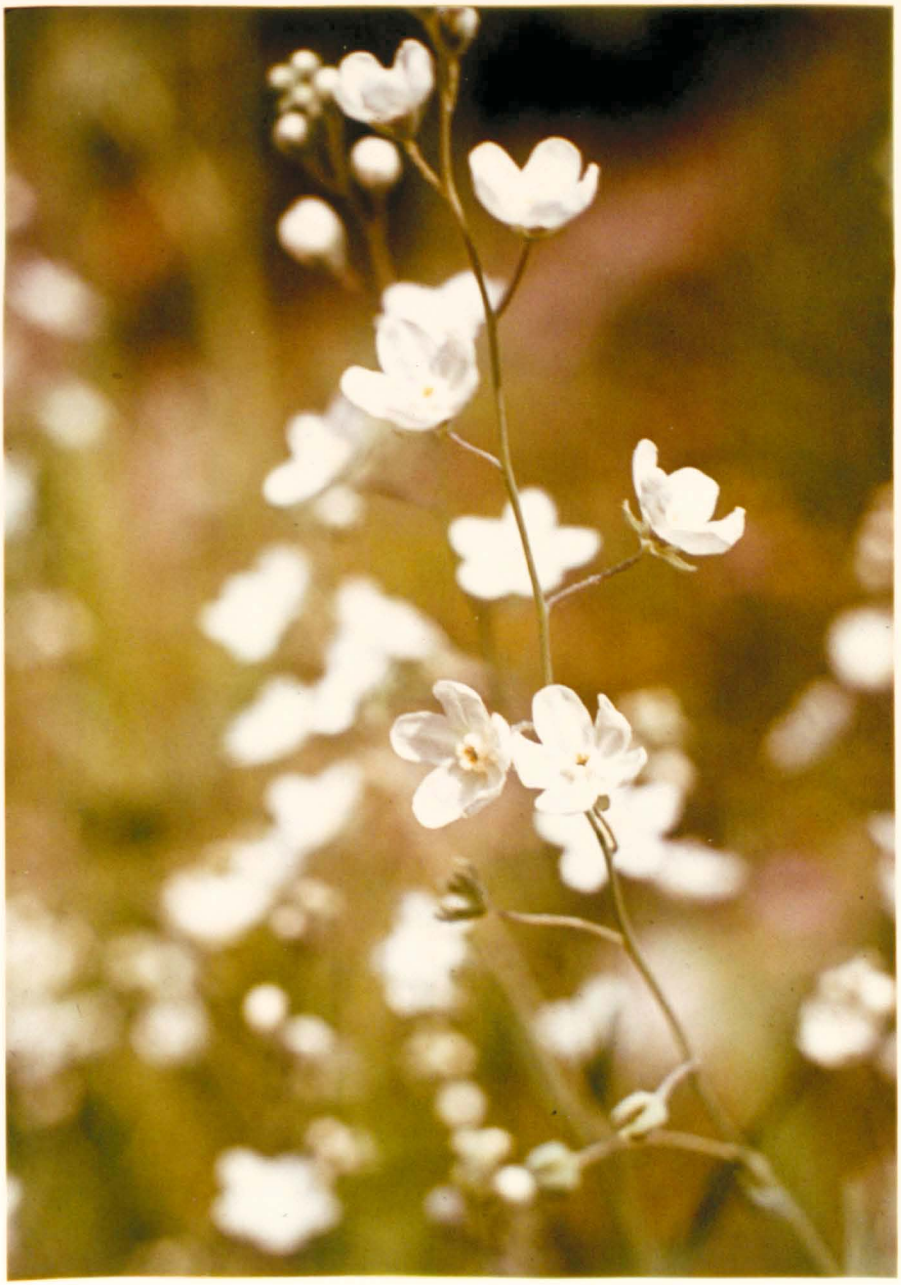


Figure 24.4

Omphalodes linifolia (Spain, prov. Malaga, Pena de Los Enamorados, 500 m, 27 April 1977, R.R. Mill 1865 (hb. E)

In all species the nutlets are ± ovate, the anterior end being narrower. Variation mainly concerns characters of the wing-like margin and of the indumentum.

The margin in subsect. Caucasicae takes the form of a narrow rim (O. kusnetzovii) or a narrow incurved wing (O. lojkae, O. rupestris). In O. rupestris the wing is said to be 'slightly dentate' (POPOV 1953) while in O. lojkae acute teeth develop and incurve. In O. cappadocica (Fig. 24.3, no. 2) the teeth are more fully developed, distant and aculeate; the wing of O. nitida (subsect. Nitidae) is very similar to that of O. cappadocica in its aculeate teeth.

In subsect. Omphalodes an entire, callous margin develops and bears a raised rim surrounding the seed. A similar but less well developed callous margin (but without the raised rim) occurs in some forms of O. cappadocica. In subsect. Lucilianthe, O. luciliae (Fig. 24.3, no.3) resembles O. verna (ic. cit., no.1) in its nutlets with entire callous margin and raised rim, while in O. ripleyana (ic. cit., no. 4) the fimbriate callous margin bears distant, aculeate incurving teeth as in O. cappadocica and O. nitida.

In sect. Candollea, O. brassicifolia (ic. cit., no. 8) has large nutlets with a relatively very narrow, almost rudimentary erect rim. O. littoralis (ic. cit., no. 7) has a similarly narrow rim, but in O. linifolia (ic. cit., no. 6) a well developed callous incurving margin with crenate rim is found, which bears a remarkable resemblance to that of Paracaryum rugulosum.

In O. scorpioides (ic. cit., no. 9) a strongly incurving flat-surfaced wing develops, forming an umbilicus; the seed is almost completely covered. (A remarkable parallel development of an umbilical, strongly incurved wing is found in the genus Desmolopha: sect. 25.3.8).

The nutlets of most species of Omphalodes possess an indumentum, although they are glabrous in O. luciliae, O. nitida and O. brassicifolia. Forms with glabrous nutlets may also occur sporadically in typically 'hairy'

species such as O. linifolia. Anchor-like glochids, as found in Cynoglossum and Paracaryum, do not occur in any species of Omphalodes as here defined.

Downy nutlets occur in subsect. Caucasicae, especially O. lojkae. the fine unicellular trichomes are sparser in O. cappadocica. Thin trichomes also occur on the nutlets of O. scorpioides and O. verna, while those of O. ripleyana are pilose on the ventral surface, more sparsely on the dorsal surface (DAVIS 1956). The latter three species cannot, however, be said to possess 'downy' nutlets.

Hooked hairs are a unique feature of the nutlets of sect. Candollea. The apex of the short, whitish-hyaline unicellular setules is sharply reflexed, forming a single barb. It can be argued that this development represents a parallel trend to the more common development of anchor-like glochids, and that they perform a similar function in nutlet dispersal. They occur in O. littoralis and most forms of O. linifolia; the nutlets of O. brassicifolia and forms of O. linifolia lack them.

24.4 PALYNOLOGY

The only detailed comparative palynological study of Omphalodes known to me is that of AVETISIAN (1956). He examined the pollen of 7 Caucasian species, including all those here referred to subsect. Caucasicae. O. caucasica Brand was considered to be distinct from O. cappadocica. His results, obtained from acetolysed pollen, are incorporated in the following account.

BARBIER & MATHEZ (1973) studied three species (O. littoralis, O. linifolia and O. nitida) using similar techniques to my own but only reported values of P and P/E. Except for O. nitida, their results are in tolerably close agreement with mine; their values of P = 9.5 μm and particularly P/E = c. 2.80 for O. nitida are, however, so different from my own that they are not considered here. Their material was labelled O. lusitanica; since

there has been confusion as to the correct application of this name it is possible that their material was wrongly identified.

I have examined pollen of the 14 species here recognised, representing all infrageneric taxa, but have not been able to study most of subsect. Caucasicae. I have therefore largely utilised Avetisian's fairly complete data in assessing the relationships of these species. All results are summarised in Table 24.2. O. kusinskyanae and O. ripleyana are palynologically unknown.

24.4.1 Description:

Pollen small (usually not exceeding 12 µm), ± constricted at equator and dumb-bell shaped, heterocolpate, tricolporate with 3 alternating pseudocolpi; apertures zonotreme. Amb hexagonal, rarely trigonal, appearing ± circular (but angular in subsect. Caucasicae). P = 7-12(-13) µm; E = 3-6.5 µm; B = 3.5-7 µm; D = 3-6.5 µm. P/E = 1.90-2.25; P/B = 1.60-1.85 (prolate); C = (100-)95-75 (very weak to very strong). Colpi usually linear, 5.5-8.5 x 0.6-1.2 µm (acetolysed, AVETISIAN, op. cit.); endoaperture an endocolpus (very rarely endoporus), 1-1.5 x 1.8-2.8 µm (AVETISIAN, op. cit.); pseudocolpi ± linear; collar absent. Sexine with ± granular or punctate LO-pattern. NPC = 345.

Within the genus, six palynological groups can be distinguished, according to the following key and descriptions.

1. Endoaperture a small endoporus ..... 6. 'scorpioides' - type
1. Endoaperture a lalongate endocolpus
  2. Amb trigonal ..... 2. 'nitida' - type
  2. Amb hexagonal
    3. Equatorial constriction strong or very strong
      (C = c. 75) ..... 3. 'verna' - type
    3. Equatorial constriction moderate to very weak (C = 95-80)
      4. P = c. 8 µm; D = less than 5 µm; C = 85-90
        ..... 4. 'luciliae' - type

4. P = 9-10 µm; D = more than 5 µm; C = less than 85 or more than 90

5. Equatorial constriction moderate

(C = 84-80) ..... 5. '*linifolia*' - type

5. Equatorial constriction slight, ± absent

(C = 100-90) ..... 1. '*lojkae*' - type

1. '*lojkae*' - type

Species included and material examined:

O. lojkae Somm. & Lev. (Caucasia: Abkhazya, Terbeda, 16 vi 1899, *Desoulavy*!).

O. kusnetzovii Kolak. (data from AVETISIAN 1956).

O. rupestris Rupr. (data from AVETISIAN 1956).

Pollen oblong, equatorial constriction absent to very weak (C = 100-90). Amb hexagonal. P = 11-13 µm; E = 6.4-6.7 µm; B = c. 7 µm (*O. lojkae*), D = c. 7 µm. P/E = 1.62-1.85; P/B = 1.60-1.80. Colpi rhombic, distinctly although narrowly diamond-shaped, bordered by muri; endoaperture a lalongate endocolpus; pseudocolpi linear; sexine ± granular.

2. '*nitida*' - type

Species included and material examined:

O. nitida Hoffmans. & Link, (Portugal: Coimbra, Matta da Balca, iv 1866, *Moller* 115!).

Pollen dumb-bell shaped, equatorial moderate (C = 86). Amb trigonal. P = 8.5-9 µm; E = 4.0-4.5 µm; B = c. 5 µm; D = 4.5-6 µm. P/E = 2.05; P/B = 1.76. Colpi ± linear, bordered by indistinct muri; endoaperture a lalongate endocolpus; pseudocolpi ± linear; sexine punctate.

The divergent values of P and P/E obtained by BARBIER & MATHEZ (1973) were not taken into account in the above description.

3. '*verna*' - type

Species included and material examined:

O. cappadocica Willd. (Turkey A6 Ordu: Ordu to Çambasi, 200 m, 6 iii 1965, *Tobey* 1512!).

O. verna Moench (Italy: Treviso, 3 km E. of Asolo, 9 iv 1960, *Davis* 34050!).

Pollen dumb-bell shaped, equatorial constriction strong or very strong (C = 76-75). Amb hexagonal. P = c. 8-10(-11) µm; E = c. 4-4.5 µm; B = c. 5-6 µm; D = c. 5-6 µm. P/E = 2.10-2.25; P/B = 1.60-1.70. Colpi linear, bordered by muri; endoaperture a lalongate endocolpus; pseudocolpi ± linear; sexine with LO-pattern.

1. P = 8.3-9.7 µm; P/E = c. 2.10 ..... verna

1. P = 9.4-10.1 µm; P/E = c. 2.25 ..... cappadocica

4. 'luciliae' - type

Species included and material examined:

O. luciliae Boiss. (Turkey C3 Antalya: Bozburun Da., above Tozlu Çukur Y., 1900-2000 m, Davis 15609!).

Pollen dumb-bell shaped, equatorial constriction moderate (C = 87). Amb hexagonal. P = 7-9 µm; E = c. 3-4 µm; B = c. 4-5 µm; D = c. 3-5 µm. P/E = 2.08; P/B = 1.80. Colpi linear, bordered by indistinct muri. Endoaperture a lalongate endocolpus; pseudocolpi linear; sexine with coarse LO-pattern.

5. 'linifolia' - type

Species included and material examined:

O. brassicifolia (Lag.) Lehm. (Spain: prov. Málaga, Sierra de Ronda, 27 v & 20 vi 1889, Reverchon 448!).

O. linifolia (L.) Moench (Spain: 3 km S. of Vejer, 50 m, 20 iv 1966, Smythies 79!).

O. littoralis Lehm. (France: sables maritimes de l'île de Hadie Marbihan, 27 v 1850, Delalande!).

Pollen dumb-bell shaped, equatorial constriction moderate to strong (C = 84-80). Amb hexagonal. P = c. 9-11 µm; E = c. 4-6 µm; B = c. 5-6 µm; D = c. 4.5-6 µm. P/E = 2.10-2.20; P/B = 1.68-1.85. Colpi ± linear; sexine with LO-pattern (rarely pattern indistinct).

1. E = 3.9-4.3 µm; P/E = c. 2.20 ..... linifolia

1. E = 4.3-5.5 µm; P/E = c. 2.10

2. P = c. 9-10 µm ..... brassicifolia

2. P = (9.8-) 10-10.6 µm ..... littoralis

6. '*scorpioides*' - type

Species included and material examined:

O. scorpioides (Haenke) Schrank (Austria: Stiria media, ad pagum Gösten prope urbem Graz, 400 m, iv 1905, *Heider* in Hayek, Fl. Stir. Exsicc. 5, 1905; 243!).

Pollen dumb-bell shaped, equatorial constriction moderate (C = 83). Amb hexagonal. P = c. 9-10 µm; E = c. 4-5 µm; B = 5-5.5 µm; D = c. 5-6 µm. P/E = 2.14; P/B = 1.75-1.77. Colpi narrowly rhombic, diamond-shaped, bordered by muri; endoaperture a small ± circular endoporus; pseudocolpi linear, bordered by muri; sexine with coarse LO-pattern.

24.4.2 *Discussion:*

With only one exception at the subsectional level, the pollen groups recognised here correspond with the infrageneric taxa proposed on the basis of morphology. Types 1-4 correspond to subgen. *Omphalodes* sect. *Omphalodes*, type 5 to subgen. *Omphalodes* sect. *Candollea*, and type 6 to subgen. *Maschalanthus*. The two subgenera differ in qualitative palynological characters. The subsections of sect. *Omphalodes* are also each characterised by a distinctive pollen type, although the differences in pollen characters at the subsectional level are more critical and tend to be quantitative. Where more than one species of a morphologically defined subsection has been examined palynologically, the members (with one exception) have similar pollen.

The only instance where the informal pollen groups cut across the proposed taxonomic subsections concerns subsects. *Omphalodes* and *Caucasicae*. As here defined, subsect. *Omphalodes* is monotypic, comprising *O. verna*, while subsect. *Caucasicae* includes *O. cappadocica*, *O. kusnetzovii*, *O. lojkae*

and O. rupestris. Of these five species, I have studied the pollen of three (O. cappadocica, O. lojkae and O. verna); all five were also examined by AVETISIAN (1956). Avetisian observed the pollen of O. cappadocica to be 11.2 x 5.6 μm. This does not compare favourably with my results (mean values, 9.7 x 4.3 μm) but may possibly be explained by technique differences. Soviet authors have often misapplied the name O. cappadocica when referring to Caucasian material; my results were obtained from authentic Turkish material of the species. Avetisian's data for O. caucasica, which he maintained separate from O. cappadocica, agree more closely with my data for O. cappadocica. A more detailed morphological and palynological study is needed for a true assessment of the status of the two taxa.

My observations show that the pollen of O. cappadocica is very different to that of O. lojkae and its allies, and is so similar to that of O. verna that I have included it in the 'verna' pollen type.

Although the morphological affinities of O. cappadocica are with O. lojkae and the two species occur sympatrically in Caucasia, while O. verna is geographically widely isolated (Alps and E. Europe), it must be admitted that O. cappadocica is rather distinct from the other species of subsect. Caucasicae. There are in fact similarities in leaf venation pattern (but not in vein number nor in elevation of veins) to O. verna, and both also show similar trends towards an undifferentiated inflorescence. O. cappadocica (which was classified in series Vernales by POPOV 1953) can perhaps be considered a transitional form between the other species of subsect. Caucasicae and O. verna. Alternatively, since O. verna and O. cappadocica are very distinct cytologically (see sect. 24.5.4) the similarity in pollen morphology may simply be the result of convergent evolution. There may be grounds for classifying O. cappadocica in a special monotypic subsection, but I hesitate to do this in the present state of knowledge; in particular, cytological information concerning the other members of subsect. Caucasicae is badly needed.

Table 24.2

Quantitative Palynological Characters of Omphalodes

All original data are based on a sample size of at least 20 grains/specimen and give mean and range (min-max). *Data of AVETISIAN (1956 - acetolysed pollen). N.M. = not measured.

Species	C	P µm	E µm	B µm	D µm	P/E	P/B
lojkae	92	12.6	c.6.5	7.0	c.6.5	1.94	1.80
lojkae*	N.M.	12.6	N.M.	7.0	N.M.	N.M.	1.80
kusnetzovii*	N.M.	11.2	N.M.	7.0	N.M.	N.M.	1.60
rupestris*	N.M.	11.5	N.M.	7.0	N.M.	N.M.	1.64
nitida	86	8.8 (8.4-9.2)	4.3 (4.1-4.5)	5.0 (4.8-5.3)	5.0 (4.6-5.7)	2.05	1.76
verna	75	9.1 (8.3-9.7)	4.3 (4.1-4.6)	5.7 (5.3-6.0)	5.2 (4.9-5.7)	2.12	1.60
cappadocica	76	9.7 (9.4-10.1)	4.3 (4.2-4.5)	5.7 (5.2-6.7)	5.3 (5.0-5.7)	2.25	1.70
cappadocica*	N.M.	11.2	N.M.	5.6	N.M.	N.M.	2.00
caucasica*	N.M.	9.8	N.M.	5.6	N.M.	N.M.	1.75
luciliae	87	8.1 (7.3-9.4)	3.9 (3.4-4.3)	4.5 (4.1-4.9)	4.1 (3.4-4.8)	2.08	1.80
brassicifolia	82	9.5 (9.1-10.2)	4.5 (4.3-4.6)	5.5 (5.2-6.0)	5.5 (5.2-6.0)	2.11	1.73
linifolia	84	9.2 (8.8-9.5)	4.2 (3.9-4.3)	5.0 (4.8-5.6)	5.2 (4.6-5.7)	2.19	1.84
linifolia*	N.M.	8.4	N.M.	5.6	N.M.	N.M.	1.50
littoralis	80	10.1 (9.8-10.6)	4.8 (4.3-5.5)	6.0 (5.3-6.4)	5.6 (5.3-5.9)	2.10	1.68
scorpioides	83	9.2 (8.7-10.2)	4.3 (4.1-4.6)	5.2 (4.8-5.6)	5.5 (5.2-5.7)	2.14	1.77
scorpioides*	N.M.	9.8	N.M.	5.6	N.M.	N.M.	1.75

Table 24.2 (contd.)

The following data ~~is~~ are from AVETISIAN (1956):

Species	Ectoaperture length μm	Ectoaperture breadth μm	Endoaperture length μm	Endoaperture breadth μm	Exine thickness μm
lojkae	8.4	1.0	1.2	2.5	0.4
rupestris	7.0	1.2	1.4	2.8	0.5
kusnetzovii	8.4	0.8	1.2	2.5	0.5
cappadocica	7.0	0.8	1.5	2.0	0.5
caucasica	7.0	0.7	1.2	2.0	0.5
linifolia	7.0	0.6	1.0	2.0	0.5
scorpioides	5.6	1.0	1.4	1.8	0.4

P = length of polar axis μm E = equatorial breadth μm B = maximum breadth μm

D = polar diameter μm C = index of constriction, E/B x 100

Of the species examined, those of subsect. Caucasicae have the least advanced pollen. The colpi are distinctly diamond-shaped and the equatorial constriction is almost absent. Trends are towards increasing constriction (culminating in the 'verna' type); towards increasing coarseness of the LO-pattern (as in O. luciliae and O. scorpioides); and change from endocolpus to endoporus (only in O. scorpioides).

24.5 CYTOLOGY

24.5.1 Introduction:

Apart from an important contribution by GRAU (1967), our knowledge of the cytology of Omphalodes is somewhat fragmentary. While most of the European species have been studied at least once, the cytology of O. luciliae, O. ripleyana and most species of subsect. Caucasicae is apparently unknown. Table 24.3 gives details of all counts of Omphalodes species known to me; all counts have been converted to the diploid form, although some were originally published as their gametic equivalent.

24.5.2 Chromosome Number:

The count of $2n = 42$, given by BRITTON (1951) for cultivated material of O. verna, is at variance with separate counts of $2n = 48$ from wild populations made by GRAU (1967) and is certainly erroneous. The count of $2n = 24$ for 'Cynoglossum linifolium' (= Omphalodes linifolia) by SUGIURA (1940) also appears to be wrong. In all other cases where the same species has been studied more than once, counts are in agreement. Races of differing chromosome number (e.g. 'cryptic polyploids') are unknown.

Four haploid numbers ($n = 11, 12, 14, 24$) and three base numbers can be detected in Omphalodes. GRAU (1967) concluded that the base numbers were: x_1 (primary) = 12; x_2 (secondary) = 11 by descending dysploidy; x_3 (secondary) = 14 ascending dysploidy. O. verna ($n = 24$) was considered to be a polyploid based on $x = 12$.

Table 24.3

Chromosome numbers in the genus Omphalodes

Infrageneric Taxon	Species	2n	Nature of source	Provenance	Reference
Subgen. Omphalodes					
Sect. Omphalodes					
Subsect. Omphalodes	verna	48	W	Italy & Jugoslavia	Grau 1967
	"	42	C		Britton 1951
Subsect. Nitidae	nitida	24	C		Britton 1951
	"	24	W	Portugal	Grau 1967
	"	24	W	Portugal	Fernandes & Leitão 1972
Subsect. Caucasicae	caucasica	22	C	Bot. Gart., München	Grau 1967
Sect. Candollea	linifolia	28	C		Strey 1931
	"	28	C		Britton 1951
	"	28	W	Portugal	Grau 1967
	"	28	W	Portugal	Fernandes & Leitão 1972
	"	24	C		Sugiura 1940
	kusinskyanae	28	W	Portugal	Grau 1967
Subgen. Maschalanthus	scorpioides	24	W	Germany	Grau 1967
	"	24	W	Czechoslovakia	Uhriková & Májovský 1978

C = cultivated material W = material of known wild origin

FERNANDES & LEITÃO (1972) observes and figured two pairs of satellite-bearing chromosomes in O. nitida (2n = 24). From this observation they deduced that Grau may have been incorrect in his assumption of 12 as primary base number in the genus. Following DARLINGTON & WYLIE (1961), they instead proposed 6 and 7 as the base numbers of the genus. They stated that the

problem would not be resolved satisfactorily until meiotic studies of plants having 2n = 24 were undertaken. In view of the prevailing occurrence of the number 2n = 24 throughout the Cynoglosseae, however, the evidence for x = 6 as a possible base number in Omphalodes is slender. It is more probable that the base numbers of the genus are 11, 12 and 14, as Grau stated; O. linifolia and O. kusinskyanae (2n = 28) both have a single pair of satellite-bearing chromosomes and so the admission of 7 as base number for these species is rendered more difficult.

24.5.3 Chromosome morphology:

The chromosomes of O. nitida, and apparently also of O. verna, are all metacentric. Similar small metacentric chromosomes occur in O. scorpioides. O. caucasica possesses a pair of large metacentric chromosomes; the other 20 chromosomes are much smaller and acrocentric. Grau thought that the two metacentric chromosomes may have been derived from the fusion of two pairs of acrocentric chromosomes.

Sect. Candollea is characterised by strong karyotypic asymmetry. Karyotypic analysis has not been attempted in detail by either GRAU (1967) or FERNANDES & LEITÃO (1972), probably on account of the small size of the chromosomes (the actual size was not stated in either paper). From the illustrations provided by the authors, however, it can be deduced that both O. linifolia (GRAU, op. cit. 69, f. 1d; FERNANDES & LEITÃO, op. cit. 399 f. 9b) and O. kusinskyanae (GRAU, op. cit. 69 f. 1e) are characterised by a single pair of satellite-bearing chromosomes, and other chromosomes of widely varying size. A mixture of metacentric and acrocentric chromosomes appears to be present in both species, with O. kusinskyanae apparently having the greater preponderance of acrocentric chromosomes.

24.5.4 Discussion:

In the present incomplete state of knowledge, any discussion of cytology and its relation to the infrageneric classification must be partly speculative.

Cytological study of subsect. Lucilianthe is a desideratum, since these species are, in some morphological aspects, transitional between sect. Omphalodes and sect. Candollea.

The available results support the classification based on morphology, outlined above. Species of different infrageneric taxa have different chromosome number. Where more than one species of a given infrageneric taxon have been studied (only example: sect. Candollea), they have the same chromosome number and similar karyotype.

The widely different chromosome numbers and differing karyotypes of O. verna and O. caucasica are interesting when compared with palynological data. O. caucasica is variously held to be either very closely allied to, or conspecific with, O. cappadocica; the latter view is held here. It has been shown that O. verna and O. cappadocica have very similar pollen and could be classified in the same pollen group. The different chromosome numbers ($2n$ = 48 in O. verna, $2n$ = 22 in O. caucasica), which are multiples of different base numbers, strongly suggest that the similarities in pollen morphology are a result of parallel evolution, rather than an indication of definite relationship. Cytological and morphological evidence supports the view held here that the species should be classified in different subsections. The data do not support Popov's inclusion of O. verna, O. nitida and O. cappadocica in the one section Arctotertiariae. (The morphological evidence against this classification has already been discussed). Cytological evidence supports the recognition of the O. linifolia group as a distinct section; the two species examined have a distinctive base number which is unknown elsewhere, not only in Omphalodes, but also in the Cynoglosseae, in the present state of knowledge.

Cytologically, the least specialised species are probably those have most chromosomes metacentric and a diploid chromosome of 24. Species included in this category are O. nitida and O. scorpioides. The diploid number 24 is very widespread in the Cynoglosseae and is also frequent in

the allied tribe Eritrichieae. The other two known diploid nembers, 22 and 28, are much rarer and of scattered occurrence outwith Omphalodes - the former is known from Paracaryum sect. Microparacaryum. Within Omphalodes, 2n = 22 is probably derived from 2n = 24 by descending dysploidy, as suggested by GRAU (1967). The origin of 2n = 28 is unknown; Grau suggested ascending dysploidy as a possible mechanism, although the intermediate state of 2n = 26 is unknown. An alternative origin might be through duplication of two pairs of non-satellite-bearing chromosomes, or by fragmentation. Detailed karyotypic analysis, which is difficult in this genus, will be the only means of resolving the problem satisfactorily. It is possible that the number 2n = 28 may have originated independently of the rest of the genus - the species of sect. Candollea are markedly different in gross morphology to those of sect. Omphalodes. O. verna (2n = 48) is almost certainly tetraploid, and thus cytologically derived; it probably arose from an ancestral form having 2n = 24.

24.6 RELATIONSHIPS

24.6.1 Intrageneric:

The distant relationships between many of the species of Omphalodes, as judged from the observations discussed in this account, have influenced me in the recognition of a relatively large number of infrageneric taxa. Several species, e.g. O. nitida and O. verna, seem to have no close allies. Except for O. cappadocica, the species of subsect. Caucasicae are closely related, however, as are those of sect. Candollea.

The least advanced species in the genus seem to be those of subsect. Caucasicae, with perennial habit, reduced gynobase (but see sect. 24.6.2), blue corollas and downy nutlets. O. nitida and O. verna are also relatively unspecialised and represent different lines of evolution from a probable 'rupestris' - type ancestor. O. luciliae and O. ripleyana are very closely related to each other but only distantly to the rest of the genus - their

nearest allies are perhaps in sect. Candollea. They form a natural ditypic group which I have recognised as subsect. Lucilianthe. EDMONDSON (1977) provides a detailed synopsis of the infraspecific classification of O. luciliae. In this balanced treatment, four largely allopatric subspecies were recognised within the extensive range of the species (Greece to Iran). O. ripleyana was maintained as a distinct species based on the differences of corolla colour, nutlet margin and degree of calyx accrescence. Sect. Candollea is undoubtedly the most advanced taxon within subgen. Omphalodes, as demonstrated by the annual habit of most of the species and the high elevated gynobase. All the species of this section are closely allied although O. littoralis is rather more distinct from the others in its morphology; the differences are probably adaptation to its coastal habitat. O. pavoniana Boiss., previously known imperfectly from the type (see BRAND, 1921), has been re-collected in Spain (prov. Salamanca) by CABALLERO (1945), but the paper, and the species, were overlooked by Flora Europaea 3 (TUTIN et al., 1972). In a recent paper, CASASECA & FERNANDEZ DIEZ (1976) drew attention to this omission and related the species to O. linifolia. I therefore include it in sect. Candollea - the photographs of the type specimen, and Caballero's gatherings, reproduced in their paper, are certainly of a plant related to O. linifolia.

24.6.2 Intergeneric:

Omphalodes occupies a rather isolated position within the tribe Cynoglosseae and in some characters is transitional to the Eritrichieae.

In habit, most species are more or less unlike other members of the Cynoglosseae. The widespread development of procumbent or creeping habit, as in subsect. Caucasicae, O. verna and O. scorpioides, has no parallel elsewhere in the tribe, although it is somewhat approached by Desmolopha. Furthermore, apart from O. nitida, tall biennials with 'Cynoglossum' habit do not occur in Omphalodes.

In floral morphology, Omphalodes somewhat resembles Cynoglossum but the corolla is more rotate. The faucal scales differ in their morphology, being distinct infoldings rather than flat scale-like appendages as in most genera of the tribe. The small nutlets arranged cross-wise on a flat gynobase, as found in most species of Omphalodes, occur elsewhere in the Cynoglosseae only in Desmolopha. The gynobase type is in fact more typical of the tribe Eritrichieae. However, the nutlet attachment is that typical of the Cynoglosseae. Sect. Candollea, unlike all other species, has a typical 'Cynoglosseae' gynobase; the nutlet attachment bears a remarkable similarity to that of Paracaryum, as was first observed by DE CANDOLLE (1846).

As mentioned above, Omphalodes seems to be a connecting link between the Cynoglosseae and the Eritrichieae. Its affinities with other genera of Cynoglosseae are uncertain - similarities to the Japanese genus Desmolopha, and to the Mexican species here referred to Mimophytum, are only partial and apparently the result of parallel evolution. The differences between these genera and Omphalodes are greater, extending to micromorphological characters, and the widespread geographical separations form the centre of Omphalodes also make it difficult to assume that there is a close natural relationship between the genera.

The dumb-bell shaped pollen of Omphalodes indicates that the genus is more specialised, palynologically at least, than genera of the Cynoglosseae having elliptic, unconstricted pollen, e.g. Cynoglossum itself. Several other morphological characters, such as the development of annual habit in some species, and the small, nearly rotate corollas, also seem to be indicative of relative advancement, although the flat gynobase is generally taken to be a non-specialised character. It is possible, however, that the flat gynobase may represent not a primitive state but the result of reduction from an elevated type. Anatomical and developmental studies of the gynobase are needed to determine the nature of its origin.

Within the Eritrichieae, several genera approach Omphalodes in habit, floral and nutlet morphology. These include Stephanocaryum, Lepechiniella

and Actinocarya. Indeed, the close similarities between these taxa and Omphalodes seem to suggest that they are more nearly related to it than it is related to other genera of the Cynoglosseae in which it is classified. This in turn suggests that the distinction between the tribes Eritrichieae and Cynoglosseae, based largely on nutlet attachment, is probably arbitrary and in need of revision (see sect. 1.3). Further studies of these and other genera of the Eritrichieae are needed in order that a fuller understanding of the tribal boundaries can be reached. Pending such an examination I have adopted a conservative treatment, assigning Omphalodes to the Cynoglosseae on the basis of its nutlet attachment, and referring the remainder to the Eritrichieae.

CHAPTER 25

17. DESMOLOPHA R. Mill

25.1 INTRODUCTION

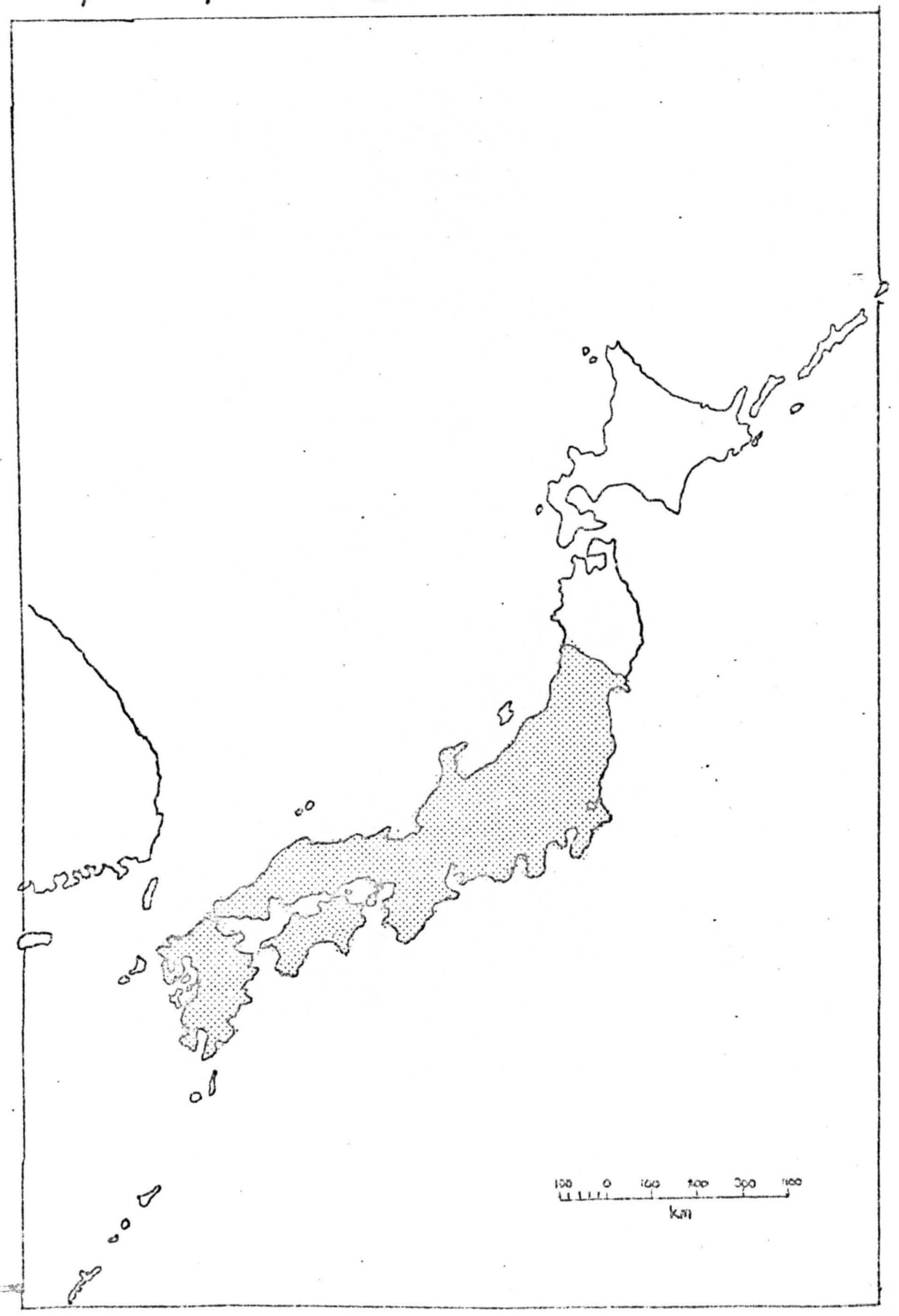
The genus Desmolopha is endemic to Japan (Shikoku, Kyushu and Honshu islands, N. to 38½° N.) and comprises three species which have hitherto been classified in the genus Omphalodes. POPOV (1953), in his account of Omphalodes, observed that the E. Asian species 'distinctly differ from the European-Caucasian ... species, representing a special subgenus', but did not award them a formal subgeneric name. On account of the many differences between these species and Omphalodes as here defined, I consider that generic rank is more appropriate. I propose the name Desmolopha, from the Greek 'desmos' (chain) and 'lophos' (crest), alluding to the form of the nutlet margin. The name is also an anagram of Omphalodes.

25.2 SYSTEMATIC TREATMENT

Desmolopha R. Mill, gen. nov.

Herbae perennes repentes pluricaules, hispido-setulosae, setis longis saepe valde inaequalibus obsitae. Rhizomates brevissimi radicibus longissimis numerosis fibrillosis. Caules numerosi, ascendentes. Folia basalia obovata usque ad spathulata, ± membranacea, in petiolum longum attenuata; caulina alterna, tota hispidissima. Racemi terminales solitares vel geminati, in parte inferiore saepius bracteati. Calyx ad basem in lobis quinque divisus, in statu fructifero paulo tantum accrescens. Corolla primum rosea deinde plerumque caerulea, subcampanulata, tubo limbum subaequante, limbo usque ad basem diviso, lobis obtusissimis non plicatis. Fornices trapeziformes, caeruleae vel violaceae. Antherae ellipticae ad ovoideae, fuscae, medifixae, filamentis brevissimis in medio tubi corollae insertae; antherae medium fornicium attingentes. Gynobasis rudimentarius, paulo convexus. Nuculae 4, ad gynobasem areola parva affixae, quam lobos calycis multo breviores, ±

Map 25,1 Distribution of Desmolophia



ovatae, umbilicatae, ala integro vel dentato ornatae, glabrae vel rariore glochidiatae.

Hispid-setulose perennial creeping herbs. Rhisomes very short, with numerous very long fibrous roots. Stems several to numerous, ascending, hispid, hairs patent, usually very unequal. Basal leaves long-petiolate, obovate to spathulate, ± membranous, attenuate at base, entire or undulate; cauline sessile, alternate, all similar, all very hispid with unequal setules. Inflorescences terminal, solitary or geminate, racemose, scorpioid, usually bracteate in lower part. Calyx divided to base, lobes ovate-oblong, hispid, hardly accrescent in fruit. Corolla rose at first, usually becoming blue, drying greyish-blue, subcampanulate, tube and limb subequal; limb divided to base, lobes obtuse, not plicate. Scales trapeziform, emarginate, blue or violet. Stamens included. Filaments very short, inserted in middle of corolla tube. Anthers elliptic to ovoid, brown, medifixed, their apices reaching middle of corolla scales. Gynobase rudimentary, slightly convex. Nutlets 4, much shorter than calyx lobes, attached to gynobase by small scar, ± ovate, umbilicate, with incurved wing-like margin; wing entire to dentate, glabrous; disc glabrous or more rarely glochidiate.

1. Nutlets with glochidiate hairs ..... 3. krameri
1. Nutlets glabrous
   2. Radical leaves 5-13 x 1.5-3 cm; setae of stem and leaves very unequal; corolla blue ..... 1. japonica
   2. Radical leaves 12-25 x 2.5-4 cm; setae of stem and leaves all ± equal; corolla rose even when mature ..... 2. prolifera

1. D. japonica (Thunb.) R. Mill, comb. nov. Syn: Cynoglossum japonicum Thunb., Fl. Japon. 81 (1784); Omphalodes japonica (Thunb.) Maxim. in Bull. Acad. Sci. Petersb. 17: 452 (1872).

2. D. prolifera (Ohwi) R. Mill, comb. nov. Syn: Omphalodes prolifera Ohwi in Bull. Nat. Sci. Mus. Tokyo 3: 98, t. 1 (1956) (n.v.).

3. D. krameri (Franch. & Savat.) R. Mill, comb. nov. Syn: Omphalodes krameri Franch. & Saval., Enum. Pl. Japon. 1: 337 (1875).
- var. laevisperma (Nakai) R. Mill, comb. nov. Syn: Omphalodes laevisperma Nakai in J. Jap. Bot. 23: 17 (1949); O. krameri Franch. & Savat. var. laevisperma (Nakai) Ohwi (place of first publication not traced, but cf. Ohwi, Fl. Japan 757: OHWI 1956b).

25.3 MORPHOLOGY

All three species of Desmolopha share a very distinctive habit and morphology, dissimilar to any species of Omphalodes, in which they were formerly classified.

25.3.1 Rootstock:

The root system is one of the most characteristic features of Desmolopha. All species are creeping perennials with short vertical or suberect rootstock and numerous long fibrous adventitious roots which branch into fibrillous rootlets. In the Cynoglosseae, similar root systems are only found in Omphalodes subsect. Caucasicae, but there they are not developed to such an extreme as in Desmolopha.

25.3.2 Stems:

The stems, which are 7-40 cm high, may be erect, ascending or arcuate-decumbent. Erect stems appear to characterise D. krameri. Those of the other two species tend to be ascending although in D. prolifera they are erect at the base (OHWI 1956a). D. prolifera tends to be taller and more robust than either of the other species. All species are always densely patent-hispid with long patent setules. In D. japonica and D. krameri the setules are very unequal, but in D. prolifera they are said to be subequal (OHWI op. cit.). In its indumentum, Desmolopha is very distinct from

Omphalodes and instead is similar to the Chinese genus Thyrocarpus Hance (here included in tribe Bothriospermeae: see sect. 28.3), and to some species of Trigonotis (tribe Trigonotideae).

25.3.4 Leaves:

Radical and cauline leaves are both numerous and well developed. The radical leaves are fasciculate, long-petiolate, and oblong or oblong-lanceolate. The petiole is frequently winged, especially in D. krameri and D. prolifera. The cauline leaves are sessile, but otherwise similar to the radical ones. The genus is characterised by the thin, membranous texture of the leaves, as well as by their densely hispid indumentum. The setules are frequently of different lengths, those of the margin being particularly long. The genus differs from other members of the Cynoglosseae in that the hairs do not arise from the tuberculate bases. In D. krameri and D. japonica the margin shows a distinct tendency to be undulate and serrate. The degree of serration varies between individual gatherings, from almost entire to quite markedly serrate.

25.3.5 Inflorescence:

The inflorescence in all species is a terminal scorpioid bracteate cyme which elongates in fruit to about double its length at anthesis. The bracts, which are confined to the lower part of the cyme and are sometimes absent in D. japonica, are oblong-ovate to broadly lanceolate, with obtuse bases. D. prolifera is characterised by the development of slightly smaller bracts in the axils of the lowest bracts when in fruit (vegetative proliferation: OHWI op. cit.).

The cymes may be simple or branched in D. krameri and D. japonica but apparently not always simple in D. prolifera. D. prolifera is also characterised by fewer flowers (4-8 per cyme) compared with the many-flowered cymes of D. japonica.

Figure 25.1

Desmolopha japonica: Morphology

1 Basal leaf, x 0.87 (Togashi 349)

2 Basal leaf indumentum, lower surface, x 35 (Togashi 349)

3 Basal leaf indumentum, upper surface, x 35 (Togashi 349)

4 Mid-length trichome from lower surface of lamina, x 85 (Togashi 349)

5 Long trichome from lower surface of lamina, x 85 (Togashi 349)

6 Short trichome from upper surface of lamina, x 85 (Togashi 349)

7 Long trichome from upper surface of lamina, x 85 (Togashi 349)

8 Stem indumentum, x 17.5 (Togashi 349)

9 Inflorescence, x 1.75 (Togashi 349)

10 Mid-length trichome with subsidiary cells, from upper surface of lamina, x 85 (Togashi 349)

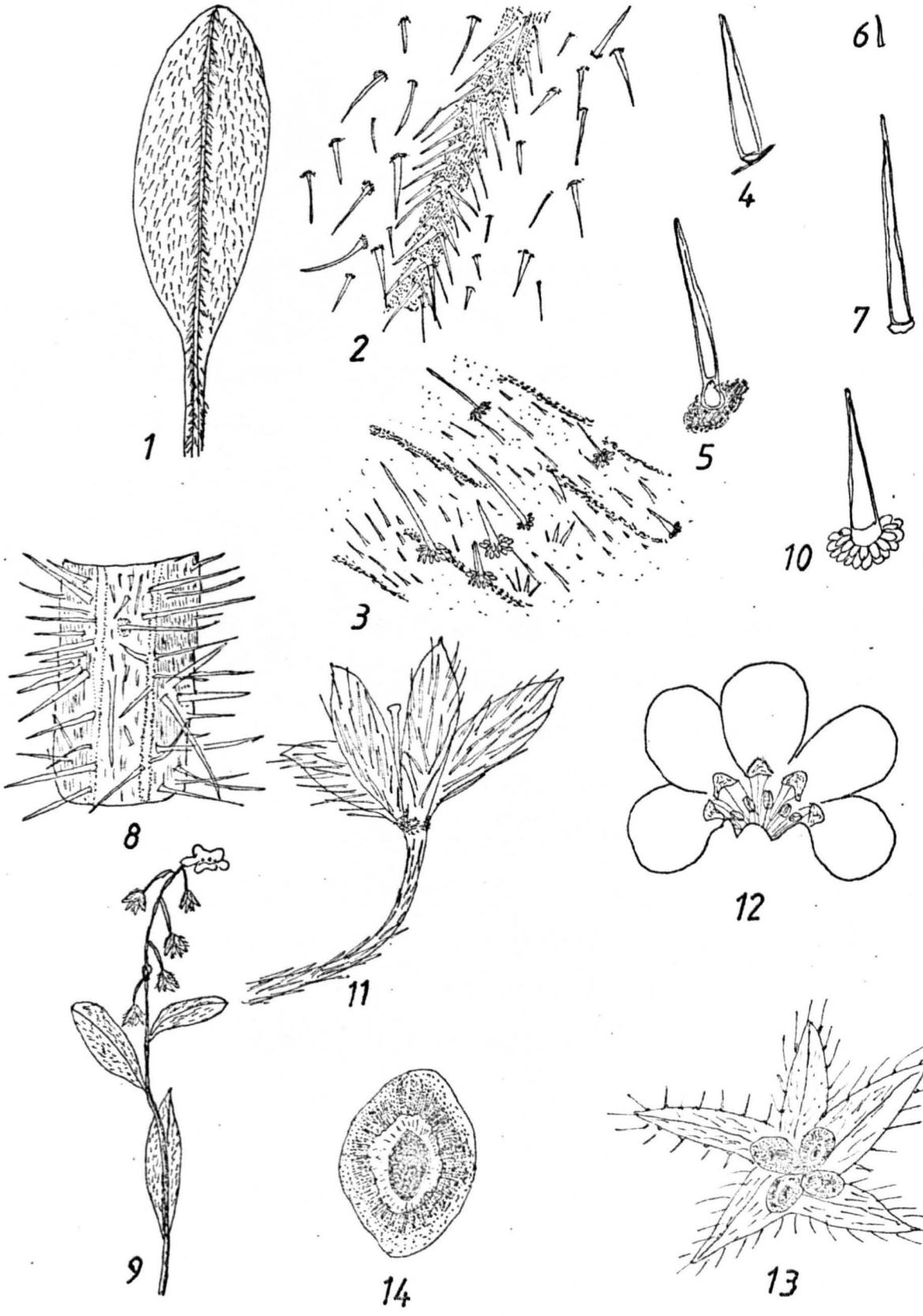
11 Calyx and pedicel, x 8.7 (Togashi 349)

12 Corolla opened out, x 4.4 (Togashi 349)

13 Calyx and nutlets, x 4.4 (Hashimoto TNS 1274)

14 Dorsal view of nutlet, x 17.5 (Hashimoto TNS 1274)

Figure 25,1



25.3.6 Calyx:

The calyx is divided to c. 4/5 or near the base into 1-veined elliptic or linear-lanceolate acute lobes. These are densely setose like the leaves. Unlike Omphalodes, accrescence in fruit is relatively slight (from 3 mm at anthesis to 5 mm in fruit in D. prolifera, according to OHWI (1956a), and from 4 mm to 6 mm in D. japonica and D. krameri). The calyx lobes become stellate-patent in fruit.

25.3.7 Corolla:

Unlike Omphalodes (except O. scorpioides) the corolla is shortly campanulate, with a fairly well developed tube subequal to the patent limb, which is divided to the base into very obtuse lobes. In D. krameri and D. japonica the corolla limb is blue, drying greyish-blue to violet. D. prolifera on the other hand has rose corollas, even at anthesis (OHWI op. cit.). The faucal scales are trapeziform and often emarginate, concolorous with the corolla lobes, and papillate. Annular scales are present at the base of the corolla in all three species, on either side of each vein-base. The anthers are elliptic-ovoid; unlike Omphalodes, their apices reach as far as the middle of the scales, although they are included in the corolla throat.

25.3.8 Nutlets:

The gynobase ('torus' of MAXIMOWICZ, 1881) is slightly convex, but rudimentary. The slightly convex shape distinguishes it from Omphalodes subsect. Caucasicae. The nutlets, which are much smaller than the calyx lobes, are attached to the gynobase by a very small apical scar, rather than the larger scar characteristic of Omphalodes.

The nutlets are ovate in outline, spherical-depressed, and calathiform, the anterior end being narrower. The margin is greatly introflexed so that the nutlet is umbilicate; the umbilicus is orbicular. D. prolifera and D. japonica have glabrous nutlets, while those of D. krameri typically have glochidiate hairs. A glabrous variety (var. laevisperma (Nakai) R. Mill)

has however been described; its status is uncertain. The presence of glochidiate hairs in D. krameri var. krameri distinguishes that taxon from Omphalodes.

25.4 PALYNOLOGY

I have examined the pollen of two of the three species of Desmolopha; material of D. prolifera was not available. Both varieties of D. krameri were studied. The results, which appear to be the first palynological information for these Japanese species, are represented below (Table 25.1).

Material examined:

D. japonica (Thunb.) R. Mill (Japan: Honshu, Tokyo, Kobotoke-toge, mt. Takao, 400 m, Togashi MT 7209!).

D. krameri (Franch. & Savat.) R. Mill:

- var. krameri (Japan: Hondo, Marakami in Yechigo, 3 v 1952, T. Tuyama & M. Togashi NSM 465!).
- var. laevisperma (Nakai) R. Mill (Japan: Honshu, Nozawamachi in Iwashiro, 9 iv 1958, M. Togashi TNS 1730! Hondo, Tsugawa in Echigo, 17 v 1957, M. Togashi TNS 1379!).

25.4.1 Description:

Pollen dumb-bell shaped, equatorial constriction weak to moderate (C = 90-82), heterocolpate, tricolporate, tripseudocolpate. Amb hexagonal, pseudoapertures included. P = c. 10-12 μm, E = c. 5-6 μm, B = c. 5.5-7.5 μm, D = c. 5.5-7 μm. P/E = 1.95-2.06, P/B = 1.68-1.78 (prolate). Colpi $\pm$ linear, bordered by bacula and furrow; endoaperture a lalongate endocolpus; pseudocolpi linear. NPC = 345. Sexine smooth.

25.4.2 Discussion:

The species of Desmolopha all have very similar pollen which cannot be distinguished by means of a key. The pollen is distinct from that of Omphalodes by the smooth exine, the colpi bordered by bacula and furrow

rather than by muri as in all species of the latter genus, and from most species by its larger size. Palynologically, Desmolopha is closer to the East Asian genera Thyrocarpus and Trigonotis, which, however, are not members of the Cynoglosseae.

Table 25.1

Quantitative Palynological Characters of Desmolopha

Species	C	P µm	E µm	B µm	D µm	P/E	P/B
japonica	86	11.1 (10.8-11.6)	5.7 (5.5-6.2)	6.6 (6.3-7.3)	6.6 (6.3-7.0)	1.95	1.68
krameri var. krameri	82	10.9 (10.5-11.6)	5.3 (5.0-5.6)	6.5 (6.0-7.0)	6.6 (6.0-7.0)	2.06	1.68
krameri var. laevisperma	89	10.5 (9.8-11.6)	5.3 (4.8-5.9)	6.0 (6.2-6.4)	6.2 (5.6-7.0)	1.97	1.76

C = index of constriction
P = length of polar axis
E = equatorial breadth
B = maximum breadth
D = polar diameter
P/E = Erdtman's ratio

25.5 RELATIONSHIPS

The relationships of Desmolopha are somewhat obscure. There are some similarities to Omphalodes, such as the umbilicate, margined nutlets and reduced gynobase, but these seem to be superficial rather than indications of real affinity with that genus. There are profound differences in habit, inflorescence, leaf morphology and indumentum, and lesser differences in corolla morphology and palynology. It seems to be closer in habit and pollen characters to the Asian genus Trigonotis and to the Chinese genus Thyrocarpus. Neither of these genera are included in the Cynoglosseae as here defined, although Thyrocarpus has previously been considered to belong to it. Despite

these similarities, Desmolopha has to be included in the Cynoglosseae on the basis of its nutlet attachment, which, apart from the small scar, is similar to Omphalodes. As with Eleutherostylum (Chapter 13), it is probable that the similarities in habit are the result of response and adaptation to similar environmental stresses.

CHAPTER 26

18. MIMOPHYTUM Greenman

26.1 INTRODUCTION

The genus Mimophytum as here redefined comprises six species, all endemic to Mexico (Map 26.1). It was described from N. Mexico by GREENMAN (1905) and then comprised the single species M. omphalodoides Greenman. The genus was characterised by tubular-campanulate corolla with 5 imbricate lobes, nutlets adpressed-glochidiate above, obliquely attached to the gynobase by an ovate-triangular scar, and by trailing habit.

Greenman, in discussing the affinities of the genus, noted a close relationship in habit and floral characters to several N. Mexican species then referred to Omphalodes, particularly to O. acuminata Robinson. He pointed out, however, that the fruit of his species 'bore a striking contrast' to the nutlet of Omphalodes, being 'more like that of Cynoglossum but ... more distinctly discoid ... with glochidiate spines on upper surface only'. He thought it best to describe his plant as a new genus based on characters of fruit and habit, and intermediate between Omphalodes and Cynoglossum.

The genus Mimophytum as here redefined includes five Mexican species formerly classified in Omphalodes, namely O. acuminata Robinson, O. aliena A. Gray, O. cardiophylla A. Gray, O. chiangii Higgins and O. mexicana Watson. The classification of these species has long been a source of mild controversy but despite the arguments they have always been formerly classified in Omphalodes. The reasons for their transfer to Mimophytum will now be outlined.

There is evidence that WATSON (unpubl.) considered the species, later named O. cardiophylla and O. aliena by Gray, to represent a new genus. Labels on sheets of these species in herb. Kew, representing isotype material,

bear the following inscriptions, written by Watson, on Gray's printed labels:

(O. cardiophylla) - - 'Leptocarya formosa Watson n. gen.'

(O. aliena) - - 'Leptocarya nudiflora Watson'.

Thus it would appear that Watson's original intention was to describe the new genus Leptocarya, with the type species L. formosa. However, there is no evidence that this genus was ever published. Watson appears to have been sceptical of Gray's classification, for, writing of these two species he states (WATSON 1883): 'the relations of these species are hardly clear. They seem to belong to Paracaryum rather than to Omphalodes ... as characterised by Bentham & Hooker, the nutlets being attached nearly their whole length, from just above the base to the apex of the erect pyramidal gynobase. The thin membranous ... flattened nutlets as well as the habit separates them from Echinospermum'. In describing O. mexicana (WATSON 1890) he again seemed to doubt that the group of species really belonged to Omphalodes, for in discussing the relationships of his new species he observed: 'evidently a congener of the plants collected by Dr Palmer in the same region and referred to this genus (i.e., Omphalodes) by Dr Gray'.

Gray's concept of Omphalodes, as set forth in his survey of N. American Boraginoideae (GRAY 1885) was very broad, including not only the European and S.W. Asian species and the Mexican taxa, but also the whole of Eritrichium: the latter is currently (and justly) recognised as a distinct genus (it is the type genus of Tribe Eritrichieae). The Mexican taxa were referred to sect. Eu-Omphalodes A. DC., which Gray distinguished from sect. Eritrichium (Schrader) A. Gray by nutlets flat or compressed, not keeled within, and with the pericarp thinly winged. Discussing O. aliena, he noted that, despite the geographical disjunction, the species had to be classified in Omphalodes on grounds of 'essential character and habit', and that, as in the S.W. European species O. linifolia and its allies

(here treated as O. sect. Candollea R. Mill), a minute lacinula of the style 'is sometimes carried away (italics mine). He considered O. cardiophylla to be allied both to O. aliena and also to sect. Eritrichium.

BRAND (1921) followed Gray in classifying all except the type species of Mimophytum as here defined, in Omphalodes sect. Eu-Omphalodes, but in his key to separate the four Mexican species then recognised from all other species of the section by their corolla with plicate lobes. As he had not seen several of the taxa, his comments are less valuable than those of American authors.

JOHNSTON (1924a) also followed Gray in classifying all taxa except M. omphalodoides in Omphalodes, but gave no reasons for his acceptance of the earlier classification. His very brief observation on M. omphalodoides is very similar in wording to Greenman's original note of 1905, as he states that 'the plant remarkably simulates the Mexican species of Omphalodes, although in technical fruiting characters it seems quite distinct and much nearer Cynoglossum'.

No revision of these taxa has ever been published, and the morphological data, though detailed, are scattered through several original papers and consequently difficult to compare. The species are in most cases known only from the type gatherings, which are also scattered in different herbaria. Despite several comments on the distinctive and anomalous nature of these species, if classified in Omphalodes, no infrageneric category has ever apparently been proposed for them under that genus. Very recently, HIGGINS (1976a) has described O. chiangii which clearly belongs to the same alliance of species, although I have not seen the type material (at TEX & WTS). Synthesis of previous data, re-examination of much of the herbarium material and original palynological research has led me to conclude that Watson was more correct than Gray in his mental recognition of the unpublished genus Leptocarya to accommodate these species.

However, the numerous, obvious morphological links with Mimophytum omphalodoides, outlined below, seem to me sufficient reason for considering that their separation at generic rank is justified. Consequently, the five taxa are here referred to Mimophytum. The only salient difference between them and M. omphalodoides is in fact the presence of winged nutlets. This difference, however, is sufficiently marked for the genus to be divided into two sections, one monotypic and comprising the type species, the other containing the five species transferred from Omphalodes.

Accepted Taxa:

M. acuminatum (Robinson) R. Mill

M. alienum (A. Gray) R. Mill

M. cardiophyllum (A. Gray) R. Mill

M. chiangii (Higgins) R. Mill (n.v.)

M. mexicanum (Watson) R. Mill

M. omphalodoides Greenman

26.2 SYSTEMATIC TREATMENT

Mimophytum Greenman in Proc. Amer. Acad. Arts Sci. 41: 242 (1905).

Type: M. omphalodoides Greenman, loc. cit. (1905).

Perennial or more usually annual herbs. Stems several, erect, ascending or trailing, slender, hollow, longitudinally striate, with patent setules or glabrescent. Leaves ± long-petiolate, broadly triangular to lanceolate, with truncate or more usually ± deeply cordiform base and acute to acuminate apex, sparingly hairy to densely villous, hairs sometimes with small calcarescent bases but lacking multicellular tubercles; upper surface often dark green and shining. Inflorescence bracteate throughout or only at base; flowers forming a pseudo-raceme, distant, solitary in axils of bracts (when bracts present). Calyx usually divided to near base (rarely to less than ½-way), lobes narrowly lanceolate or ovate. Corolla usually white, rarely rose or pale blue, rotate to campanulate, lobes plicate,

imbricate. Faucal appendages (scales) prominent, subexserted, shallowly emarginate, minutely papillose. Anthers oblong-ovoid, with their bases borne below bases of scales. Style shorter than calyx in flower but exceeding the mature nutlets. Nutlet solitary by abortion in some species, 2-4 developing in others, attached to pyramidal gynobase by subapical lanceolate scar, either unwinged and glochidiate or with incurving wing and then lacking spines; puberulent.

1. Nutlets unwinged, densely covered with glochidiate spines (Sect. Mimophytum) ..... 1. omphalodoides

1. Nutlets with entire to dentate wing, lacking glochidiate spines (Sect. Pterocaryum)

2. Leaves with short ± scattered hairs on both surfaces, upper surface ± dark green and shining

3. Wing of nutlet entire ..... 4. chiangii

3. Wing of nutlet denticulate, with c. 30 trilobed teeth ..... 2. acuminatum

2. Leaves densely villous, at least on lower surface

4. Upper surface of leaves very sparsely setulose .. 3. cardiophyllum

4. Upper surface of leaves almost as densely villous as lower

5. Inflorescence bracteate throughout; leaves ovate to broadly lanceolate, (5-) 12-17 mm broad ..... 5. mexicanum

5. Inflorescence bracteate only near base; leaves broadly triangular, 20-45 mm broad ..... 6. alienum

Sect. Mimophytum. Trailing annual herb. Nutlets unwinged, with long glochidiate spines.

1. M. omphalodoides Greenman, loc. cit. (1905).

Sect. Pterocaryum R. Mill, sect. nov. Syn: Omphalodes Miller sect. Eu-Omphalodes A. DC. in DC., Prodr. 10: 161 (1846) sensu A. Gray in Proc.

Amer. Acad. Arts Sci. 20: 262 (1885) p.p. quoad plantas mexicanas; 'Leptocarya' W.C. Watson in sched. kewens., nom. invalidum, pro gen.

Herbae perennes vel annuae adscendentes aut procumbentes nuculis alatis sine spinulis glochidiatis; ala nuculae ± incurvata, integra vel plerumque denticulata vel dentata.

Annual or perennial herbs, ascending or trailing, with winged nutlets lacking glochidiate spinules; wing of nutlet ± incurving, entire or usually denticulate or dentate.

Type: M. cardiophyllum (A. Gray) R. Mill.

2. M. acuminatum (Robinson) R. Mill, comb. nov. Syn: 'Omphalodes acuminata' Watson in sched. kewense, nom. nud.; O. acuminata Watson ex Robinson in Proc. Amer. Acad. Arts Sci. 26: 170 (1891).

3. M. cardiophyllum (A. Gray) R. Mill, comb. nov. Syn: Omphalodes cardiophylla A. Gray ex Hemsl., Biol. Centr. Amer., Bot. 2: 377 (1882); 'Leptocarya formosa' Watson in sched., nom. nud.

4. M. chiangii (Higgins) R. Mill, comb. nov. Syn: Omphalodes chiangii Higgins in Phytologia 33: 412 (1976).

5. M. mexicanum (Watson) R. Mill, comb. nov. Syn: Omphalodes mexicana Watson in Proc. Amer. Acad. Arts Sci. 25: 158 (1890).

6. M. alienum (A. Gray) R. Mill, comb. nov. Syn: Omphalodes aliena A.Gray ex Hemsl., Biol. Centr. Amer., Bot. 2: 377 (1882); 'Leptocarya nudiflora' Watson in sched., nom. nud.

26.3 MORPHOLOGY

All the species of Mimophytum are more closely related to one another morphologically than any is to supposedly allied genera such as Omphalodes or Cynoglossum. The taxa are evolutionarily derived and none shows any obviously primitive characteristics.

26.3.1 Rootstock:

Relatively little is known about the rootstock of the members of the

genus, information being confined to that in the type description and the small fragments preserved on some herbarium sheets. In M. alienum and M. mexicanum it is relatively short, ± stout and erect to subhorizontal. The remaining species show varying degrees of development of a procumbent, slender stock with ± distant nodes which apparently do not develop adventitious roots. M. acuminatum and M. omphalodoides represent culminations of this trend.

26.3.2 Stem:

Stem and root habit are closely inter-related. Two divergent groups can be recognised:

a) low, erect to ascending herbs with numerous, sparsely branched stems (M. alienum and M. mexicanum). This group is also characterised by erect to subhorizontal, short rootstocks.

b) plants with fewer, longer, trailing stems with diffusely branching habit (M. cardiophyllum, and especially M. omphalodoides and M. acuminatum; M. chiangii is said to have decumbent or trailing stems and therefore probably also belongs here). This group also has procumbent rootstocks.

Species characterised by trailing habit also tend to have less hairy stems than those which are erect to ascending. M. alienum and M. mexicanum both have ± dense, shaggy, villous stems, the hairs in the lower part being especially long and patent. M. cardiophyllum, which appears to be semi-trailing, retains a similar villous indumentum, but in M. omphalodoides and M. acuminatum the indumentum is reduced to sparse patent setules, the stems later becoming subglabrous.

26.3.3 Leaves:

In most species there is no marked differentiation into radical and cauline leaves. Radical leaves were described for O. cardiophylla by GRAY (1882) but they were not present on isotype material at Kew. Gray may have described the lowest cauline leaves.

Almost all the species are characterised by cordiform leaves with a ±

well-developed basal sinus. In most species the leaves are not strictly cordate since the tissue of the basal sinus curves right round to merge into the winged petiole, which tends to be broadest at its poorly-defined junction with the base of the lamina. Cordiform leaves are especially well developed in M. omphalodoides, M. acuminatum, M. cardiophyllum and in M. chiangii (fide HIGGINS 1976a). M. alienum has broadly triangular leaves, while those of M. mexicanum are broadly lanceolate to ovate; both these species have truncate, not cordiform, leaf bases. The cordiform leaf base is thus strongly correlated with trailing habit, in the specimens examined.

Also apparently correlated with the cordiform base is an acuminate apex; such apices are especially well developed in M. omphalodoides and M. acuminatum, less so in M. cardiophyllum. HIGGINS (1976a) described the apex in M. chiangii as acute to shortly acuminate, while that of M. alienum is somewhat suddenly acuminate, and that of M. mexicanum is acute.

In the species studied, all principal veins radiate from the base of the lamina. In M. acuminatum and M. omphalodoides the venation is brochidodromous or almost so, while in M. mexicanum and M. alienum it is camptodromous (Fig. 2.4, nos. 9-12).

In all species the leaf indumentum is denser on the lower surface of the lamina. The most hairy leaves are found in M. alienum and particularly M. mexicanum. In these species the leaves are villous, the hair bases lacking subsidiary cells and not or only slightly calcarescent. In M. cardiophyllum, there is greater differentiation between upper and lower surfaces, the former being very sparsely setulose, the latter retaining a dense, greyish villous indumentum. The trichome bases on both surfaces, unlike M. alienum and M. mexicanum, have pustular bases surrounded by a single row of subsidiary cells, but the trichomes are not markedly impressed into the lamina.

In contrast, villous indumentum is entirely lacking in M. omphalodoides

and M. acuminatum. In both these species the upper surface of the lamina is deep green and shining with sparse setules strongly impressed into the lamina, glabrescent, and with calcarescent trichome bases, while the lower surface is dull pale green with more numerous scattered setules surrounded by a ring of subsidiary cells and with calcarescent bases.

The subsidiary cells in Mimophytum are small and circular, somewhat similar to those of Paracaryum but much smaller and less pronounced, and are of a type not found in Omphalodes. They are distinct from those found in the endemic Mexican genus Madrea, in which the stout setules are surrounded by up to 3 concentric rings of narrowly oblong subsidiary cells.

M. omphalodoides, M. acuminatum and M. mexicanum are characterised by the development of long slender petioles which may exceed the lamina in length; the remaining species have shorter petioles. The petiole is ± winged and decurrent into the stem in M. mexicanum, M. alienum and M. cardiophyllum, but neither of these features is shown by M. acuminatum or M. omphalodoides.

26.3.4 Inflorescence:

The inflorescence is normally undifferentiated and bracteate throughout, a condition found in all investigated species except M. omphalodoides and M. alienum. In these species have a terminal differentiated inflorescence, bracteate only at the base. M. chiangii is unsatisfactorily described in this respect by HIGGINS (1976a) as having the 'inflorescence bracteate', and therefore could fall into either category.

In most taxa the individual cymes consist of a single flower by reduction, and are borne in the axils of bracts resembling smaller cauline leaves. In species with a differentiated inflorescence they are arranged in a pseudo-raceme which greatly lengthens at maturity.

26.3.5 Pedicels:

Extreme development of the pedicels is a feature of the genus. In most species the pedicels are many times the length of the calyx, often

exceeding the bracts, and are slender, becoming flexuous-patent in fruit. The indumentum resembles that of the upper part of the stem, being usually adpressed-strigillose.

26.3.6 Calyx:

The calyx is regularly 5-lobed and accrescent in fruit. In most species the lobes extend nearly to the base; M. cardiophyllum is exceptional in having very short lanceolate-ovate lobes only 1/5 the total length of the calyx at anthesis. Calyx accrescence is most marked in M. acuminatum and M. omphalodoides, least in M. alienum and M. mexicanum. In all species the calyx is adpressed-strigillose, trichome colour being grey to silvery or bluish.

26.3.7 Corolla:

The corolla is normally subrotate, with a short tube often included in the calyx, and a short but broadly patent limb. The tube is particularly short, and the corolla rotate, in M. cardiophyllum and M. acuminatum, the latter species has by far the largest corollas of the genus (Fig. 26.1, nos. 7 & 8). The limb is lobed to at least halfway, and almost to the base in some taxa, e.g. M. acuminatum. The lobes are plicate and have large rounded sinuses between them.

There is evidence from collector's labels and original descriptions that the flowers of some species are coloured when fresh, but the corollas of all species are ± white when dry. M. omphalodoides (Fig. 26.1, nos. 5 & 6) has pale blue flowers in vivo, and traces of blue colouration are sometimes preserved. M. alienum (Fig. 26.1, nos. 9 & 10) also has pale blue corollas in the living state, while ROBINSON (1891) described the fresh colour of the corolla in M. acuminatum as rose. In the other species, the corolla is apparantly white in vivo as well as in sicco. Boiled corollas remain ± white, except in M. omphalodoides where they change to a greyish blue colour. The bright yellow colour change observed in Omphalodes sect. Candollea does not occur.

Figure 26.1

Mimophytum: Floral and Fruit Morphology

1 M. omphalodoides, dorsal view of nutlet, x 8.7 (Palmer 8822)

2 M. acuminatum, dorsal view of nutlet, x 8.7 (Pringle 10162)

2a marginal teeth of nutlet wing, x c. 85

3 M. alienum, group of nutlets, x 13 (Pringle 10206)

4 M. mexicanum, dorsal and dorso-lateral views of nutlets, x 13 (Pringle 2697)

5 M. omphalodoides, corolla, x 4.4 (Palmer 8822)

6 M. omphalodoides, corolla opened out, x 4.4 (Palmer 8822)

7 M. acuminatum, corolla, x 2.6 (Pringle 10162)

8 M. acuminatum, corolla opened out, x 2.6 (Pringle 10162)

9 M. alienum, corolla, x 2.6 (Pringle 10205)

10 M. alienum, corolla opened out, x 2.6 (Pringle 10205)

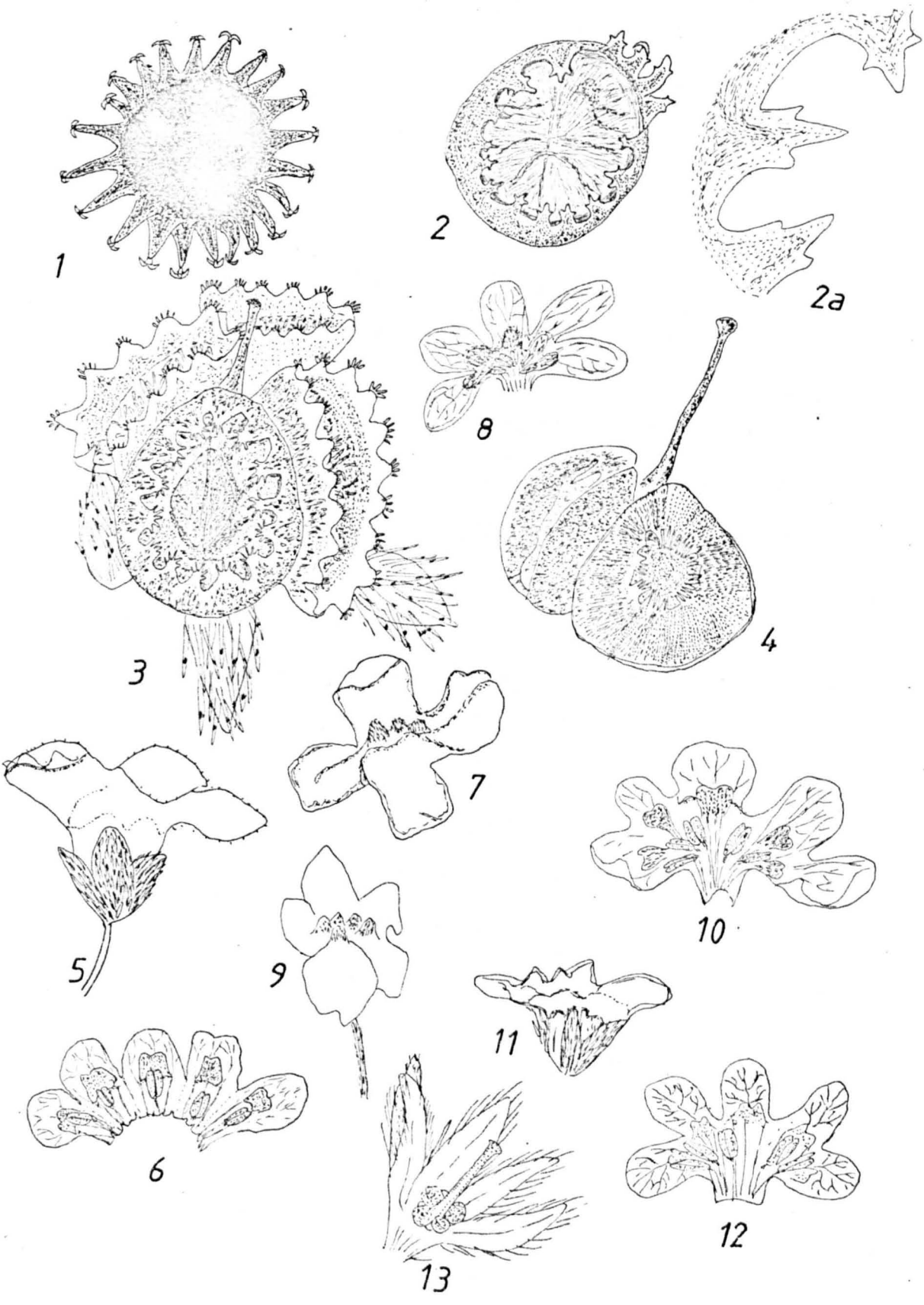
11 M. mexicanum, corolla, x 4.4 (Pringle 2697)

12 M. mexicanum, corolla opened out, x 4.4 (Pringle 1878)

13 M. omphalodoides, calyx and style, x 8.7 (Palmer 8822)

(Leaves are illustrated on Figure 2.4)

Figure 26,1



Faucal scales are well developed and are just exserted, closing the throat. They are trapeziform with broader 2-lobed bases, the lobes divergent and tapering; the apical portion is shallowly emarginate and minutely papillose. The scales are concolorous with the corolla in all species examined, although they appear darker than the lobes when dry. Annular scales are not developed at the base of the corolla tube.

The anthers are alliptic to ovoid, medifixed on short filaments inserted in the corolla tube below the scales. The whole anther is situated below the scale base in most specimens, but in some flowers of some species, e.g. M. acuminatum, the apex may extend to the middle of the scales.

26.3.8 Nutlets:

Abortion of one or more nutlets is a feature of most species of Mimophytum. Only in M. alienum (Fig. 26.1, no. 3), apparently, do all 4 nutlets regularly mature; even in this species, individual gynobases may have 3 or fewer nutlets. In M. chiangii 2-4 nutlets develop (HIGGINS 1976a) while in M. cardiophyllum 1-3 develop. In the remaining three species there is normally a solitary ripe nutlet, although 2 may rarely mature in M. mexicanum.

In all species the gynobase is shortly pyramidal and the nutlets are subapically attached by a lanceolate ventral scar. In this respect the genus sharply differs from Omphalodes (except sect. Candollea), which is also very different in all aspects of its vegetative morphology. The nutlets of Mimophytum are subequal to the gynobase and exceed the deflexed calyx lobes.

As in Omphalodes, the principal trend concerns the evolution of a wing-like margin. Presence or absence of a thickened wing has been used in sect. 26.2 to divide the genus at the sectional level. M. omphalodoides is unique in the absence of a wing and in the development of glochidiate spines. Earlier authors have commented on the similarity of the nutlet

of this species to that of some species of Cynoglossum (sensu lato). In form, the nutlet of M. omphalodoides comes closer to the type found in Paracynoglossum and is wholly unlike that of Cynoglossum as here defined. From Paracynoglossum (all species of which are wholly unrelated to Mimophytum) the nutlet differs in being more strongly flattened, and by the presence of spines on the dorsal surface only. The similarity to Paracynoglossum is only superficial and must not be weighted heavily when discussing the intergeneric relations of Mimophytum.

The nutlets of all species of sect. Pterocaryum possess an incurving wing. These species were formerly included in Omphalodes, apparently on the strength of this character alone. The many differences between Mimophytum and Omphalodes have already been high-lighted, as has the fact that many other species have also been wrongly classified in Omphalodes simply because their nutlets have a rim-like wing. It would appear that superficially similar nutlets have developed several times in spatially and taxonomically separated genera, possibly in response to similar environmental conditions.

All species of sect. Pterocaryum examined have the wing minutely puberulent. The hairs are slender and unicellular. Similar hairs also occur sparsely on the dorsal surface of the nutlet of M. omphalodoides intermixed with the spines. Hooked hairs, as found in Omphalodes sect. Candollea, do not occur.

In all species except M. chiangii the wing is ± dentate. M. chiangii is said to have an entire wing; this is probably a derived condition but material needs to be examined.

In M. mexicanum and M. cardiophyllum, the teeth are simple and acute, lacking appendages. M. acuminatum and M. alienum, however, are remarkable in the development of the teeth. Those of the former (Fig. 26.1, no.2a) are trilobed, with two short blunt median appendages and a longer, tapering,

subobtuse terminal lobe, while in M. alienum each tooth bears a cluster of 4-5 thickened, obtuse projections at the tip (Fig. 26.1, no. 3). These are much shorter and relatively more thickened than glochids, and lack anchor-like barbs.

26.4 PALYNOLOGY

The pollen of all species except M. chiangii has been examined and is here described for the first time. Quantitative results are summarised in Table 26.1.

26.4.1 Description:

Pollen small (not exceeding 12 μm), oblong, constricted (often very strongly) at equator, dumb bell or bone-shaped, poles often angular in equatorial view; heterocolpate, tricolporate with 3 alternating pseudocolpi. Amb trigonal, convex, acute, appearing ± circular. P = c. 8-12 μm, E = c. 3-5 μm, B = c. 5-6 μm, D = c. 4-6(-6.5) μm. P/E = 2.17-3.24; P/B = 1.65-1.85 (pollen prolate); C = 79-55 (strong to extremely strong). Colpi narrowly rhombic, ± linear, sometimes indistinct and appearing as though absent; endoaperture an endocolpus (sometimes ± circular); pseudocolpi linear, apparently unbordered; collar absent. Sexine smooth or with LO-pattern. NPC = 345.

1. C strong (c. 79-76); P/E less than 2.30; E = 3.5-5 μm
..... 'omphalodoides' - type

1. C very strong or extremely strong (c. 75-55);
P/E greater than 2.50; E = 2.8-4.5 μm ..... 'cardiophyllum' - type

1. 'omphalodoides' - type

Species included and material examined:

M. alienum (A. Gray) R. Mill (Mexico: Nuovo Leon, hills nr Monterey, 6 iii 1906, Pringle 10205! ibid., 6 iv 1906, Pringle 10206!).

M. mexicanum (Watson) R. Mill (Mexico: Nuovo Leon, nr Monterey, 1 iv 1889, Pringle 2697!).

M. omphalodoides Greenman (Mexico: Puebla, nr Honey Station, 24 v 1905, Pringle 8822!).

Pollen with strong equatorial constriction (C = 79-76); P = 8-11.5 m; E = 3.5-5 m; B = 5-7 m; D = 4-6.5 m. P/E = 2.17-2.22; P/B = 1.65-1.75.

1. Colpi distinct, bordered by furrow and indistinct bacula ..... alienum

1. Colpi indistinct or almost invisible, bordered apparently by bacula only

2. Sexine with coarse LO-pattern; endocolpus bordered by murus ..... mexicanum

2. Sexine ± smooth; endocolpus unbordered ..... omphalodoides

2. 'cardiophyllum' - type

Species included and material examined:

M. acuminatum (Robinson) R. Mill (Mexico: Nuovo Leon, nr Monterey, 10 iii 1906, Pringle 10162!).

M. cardiophyllum (A. Gray) R. Mill (Mexico: Coahuila, nr Saltillo, viii 1880, Palmer 894!).

Pollen with very strong to extremely strong equatorial constriction (C = c. 72-55); P = 9-10 m; E = 3-4 m; B = 5-6 m; D = 4-6 m. P/E = 2.56-3.24; P/B = 1.77-1.84.

1. C = c. 70; P/E less than 3.00; colpi indistinct ..... acuminatum

1. C = c. 55; P/E more than 3.00; colpi narrowly rhombic bordered by very indistinct bacula ..... cardiophyllum

26.4.2 Discussion:

The five species examined are closely similar in their pollen morphology and a palynological division of the genus is possible only by using quantitative characters. The two groups proposed largely comprise species of close morphological affinity but they somewhat cut across the formal

classification of the genus as outlined above.

Especially noteworthy is the similarity in the pollen of M. omphalodoides to that of M. mexicanum and M. alienum. M. omphalodoides is most closely allied morphologically to M. acuminatum and it might be expected, therefore, that these two taxa would also possess similar pollen. This is not the case, however. Although the pollen resembles M. acuminatum and M. cardiophyllum in its indistinct colpi, the equatorial constriction is much less pronounced than in either of those taxa and is of the order of that found in M. alienum. Reticulate evolution, a feature of the Boraginaceae, may help to explain this somewhat anomalous palynological relationship.

Although all three genera have dumb-bell shaped pollen, that of most species of Mimophytum differs from both Omphalodes and Madrea in having the poles angular in equatorial view. The very high values of P/B in some taxa are unknown in either of the other two genera and are the highest values which I have recorded in my studies of the Cynoglosseae.

26.5 RELATIONSHIPS

The affinities of Mimophytum are somewhat uncertain. Morphologically and palynologically the genus is extremely distinct from other extant Mexican taxa of Cynoglosseae. Assessment of relationships is further hindered by the highly derived morphology, and by the fact that Mexican taxa are in general rather imperfectly known and sparsely represented in British herbaria.

There seem to be distant affinities with Omphalodes but the similarities between the two genera are outnumbered by the differences and are more likely to be the result of convergent evolution. Gray and others have related the species here assigned to sect. Pterocaryum to O. linifolia, on the basis of similarity of nutlet attachment, but the vast differences, in life form, vegetative morphology (e.g. the cordiform leaves - in this character, Mimophytum stands almost alone in the Cynoglosseae), indumentum type and

Table 26.1

Quantitative Palynological Characters of Mimophytum

Species	C	P μm	E μm	B μm	D μm	P/E	P/B
omphalodoides	79	9.1 (8.4-9.8)	4.1 (3.5-4.3)	5.2 (4.9-5.7)	5.3 (4.9-5.6)	2.22	1.75
alienum	77	9.6 (8.5-11.5)	4.4 (3.5-5.0)	5.7 (4.8-6.7)	5.3 (4.3-5.9)	2.18	1.69
mexicanum	76	9.1 (8.3-9.5)	4.2 (3.6-4.6)	5.5 (4.8-6.2)	6.4	2.17	1.65
acuminatum	72	9.2 (8.8-9.5)	3.6 (3.2-4.3)	5.0 (4.8-5.9)	4.9 (4.2-5.7)	2.56	1.84
cardiophyllum	55	9.4 (9.0-9.9)	2.9 (2.8-3.4)	5.3 (4.9-5.9)	4.9 (4.3-5.3)	3.24	1.77

C = index of constriction $\frac{E}{B}$ x 100 P/E = Erdtman's ratio

P = length of polar axis E = equatorial breadth

B = maximum breadth D = polar diameter

Sample size: all except M. alienum: one preparation, mean of 10 grains

M. alienum: two preparations, mean of 10 grains from each.

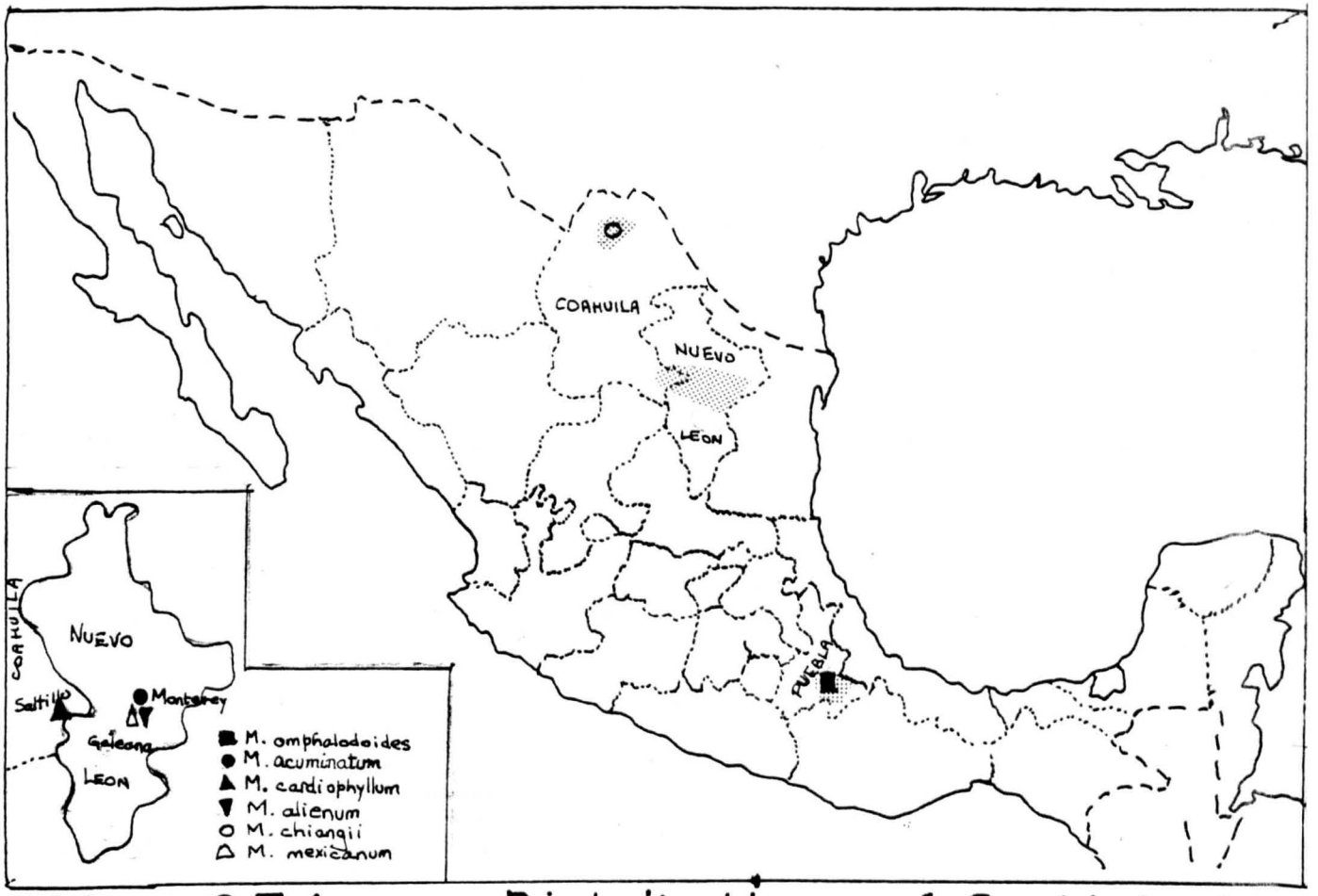
The two specimens showed insignificant variation between them.

floral pigmentation preclude any close relationship. Similar 'affinities' between M. omphalodoides and Cynoglossum have been shown above to be merely superficial. It must be noted, however, that Austrocynoglossum latifolium (R. Br.) R. Mill (= Cynoglossum latifolium R. Br.) has also evolved a semi-trailing habit with somewhat cordiform leaves, and axillary, solitary long-pedicellate flowers arranged in an undifferentiated, bracteate inflorescence (see Chapter 23), but as this is an Australian genus the likelihood of a direct affinity with Mimophytum is extremely improbable.

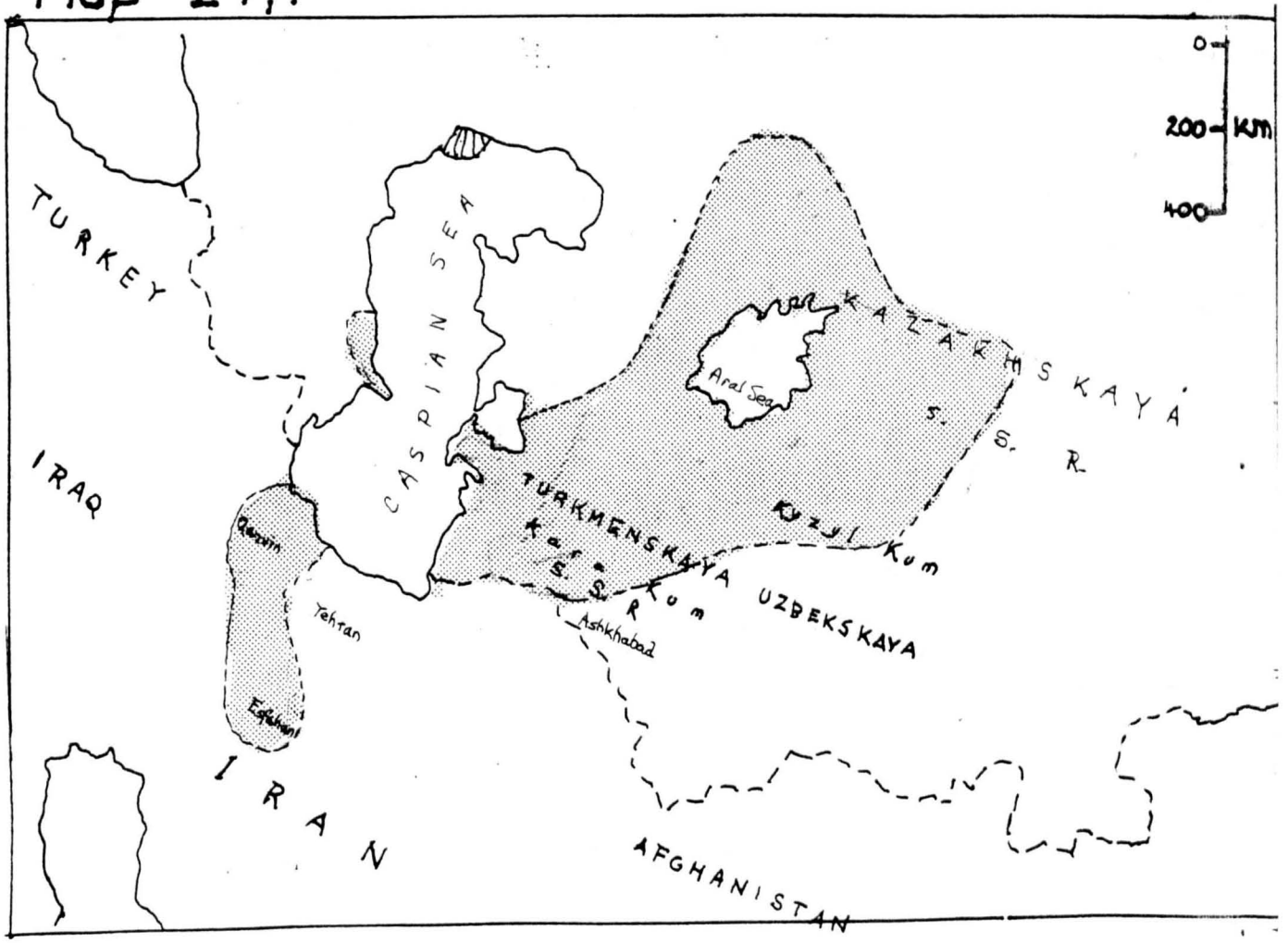
The affinities of Mimophytum with the Mexican endemic, Madrea erecta, are even more distant. The two taxa differ markedly in life-form, Madrea being a stiffly erect perennial with somewhat harsh indumentum like that of Paracynoglossum, and with a completely different leaf shape and venation to Mimophytum. The nutlet of M. erecta has a broad spreading wing totally unlike that found in any species of Mimophytum.

In the present state of knowledge, therefore, it is probably best to consider Mimophytum as an endemic genus of isolated, somewhat uncertain taxonomic affinity within the tribe Cynoglosseae.

Map 26,1 Distribution of Mimophytum



Map 27,1 Distribution of Suchtelenia



CHAPTER 27

19. SUCHTELENIA Karelin ex Meisner

27.1 INTRODUCTION

The genus Suchtelenia is ditypic. The two species are confined to Iran, Turcomania, Transcaucasia and Transcaspia (Map 27.1).

Although it is a well-defined, natural genus, the affinities of Suchtelenia are uncertain and its tribal position has been disputed. BRAND (1921), following BENTHAM & HOOKER (1876), included it in the Cynoglosseae, where it was placed at the end of his sequence of genera. ZAKIROV (1941) removed it to the tribe Trichodesmeae on account of its markedly accrescent calyx, a character which in his opinion related it to Trichodesma and Caccinia. Recent authors, including POPOV (1953) and RIEDL (1967), have tended to favour this view, although Popov qualified his treatment by saying that the genus was 'usually referred to the Cynoglosseae'. Palynological studies by BARRIER & MATHEZ (1973), however, led them to question this relationship. They found that Suchtelenia had small dumb-bell shaped pollen similar to that found in many genera of Cynoglosseae and Eritrichieae, whereas the pollen of Trichodesma and Caccinia was among the largest in the family, resembling that of Borago in size but differing by being 3-aperturate.

The morphological and palynological data strongly suggest that Suchtelenia is incorrectly classified in the tribe Trichodesmeae and that it should be re-instated as a member of the Cynoglosseae. Recently, KAZMI (1975) described the genus Ivanjohnstonia (see Chapter 21), an undoubted member of the Cynoglosseae close to Paracynoglossum but which has a somewhat similar markedly accrescent calyx. The calyx of Asperugo is also very strongly accrescent, but it is not placed in the Trichodesmeae; rather, it is usually classified in the Eritrichieae, or in the monogeneric tribe Asperugeae. It appears that the accrescent calyx has evolved independently

in Asperugo, Suchtelenia, Ivanjohnstonia and the Trichodesma - Caccinia group.

Accepted Taxa:

S. calycina (C.A. Meyer) A. DC.

S. eriophora Bornm.

27.2 SYSTEMATIC TREATMENT

Suchtelenia Karelin ex Meisner, Gen. Comm. 188 (1840).

Type: S. calycina (C.A. Meyer) A. DC.

Annual herbs. Rootstock thin, vertical. Stems erect to ascending, to 30 cm, simple or branched from base, striate, glabrous, tuberculate or white-pilose. Lower leaves opposite, median and upper alternate, ovate-oblong, or spathulate, obtuse, fleshy, subglabrous or hairy beneath, pilose or with scattered white tubercles on upper surface, tubercles bearing very short, soon caducous setules; margins setulose. Inflorescence of terminal bracteate cymes, greatly elongating in fruit. Calyx divided to c. $\frac{1}{2}$-$\frac{3}{4}$, 2-3 mm in flower, markedly accrescent to c. 12 mm diam. after flowering, deciduous in fruit along with the nutlet; lobes in flowering state either linear-lanceolate or obtuse-triangular. Corolla sky blue or purple, 2.5-5 mm diam., shortly and broadly infundibular. Faucal scales small, shortly triangular, broader than long, thickened at apex. Stamens inserted in middle of tube; filaments short; anthers small, broadly ovoid, apices reaching bases of scales. Style very short and rather fat, c. 0.5 mm long. Gynobase large, ovoid, with 4 crests alternating with nutlets. Nutlets usually solitary (-2) by abortion (S. calycina) or 4 (S. eriophora), attached to gynobase by a scar occupying most of the ventral surface, dimorphic, 1-2 persistent, becoming horizontal, ovoid, the others not developing to maturity but abscissing easily when immature, oblong; dorsal

surface of nutlets smooth or ± glochidiate, sometimes also with white hairs (S. eriophora).

1. Plant with long patent white hairs; calyx lobes linear-lanceolate in flower; corolla 5 mm long, purple ..... 2. eriophora

1. Plant ± glabrous or with scattered setules; calyx lobes obtuse-triangular in flower; corolla c. 2-3 mm long, sky blue .... 1. calycina

2. Nutlets smooth or with few spinules in a line along dorsal surface; corolla c. 4 mm diam. ..... var. calycina

2. Nutlets densely spinulose on dorsal surface; corolla c. 5 mm diam. ..... var. acanthocarpa

1. S. calycina (C.A. Meyer) A. DC. in DC., Prodr. 10: 163 (1846).

Several taxa have been described within S. calycina, and some, e.g. S. acanthocarpa Kar., have been treated as species. Most recent authors treat them as varieties or races; RIEDL (1967) recognises the two following varieties, which are keyed out above:

var. calycina (Fig. 18.1, no. 8)

var. acanthocarpa (Kar.) O. Kuntze in Acta Horti Petrop. 10: 218, 219 (1887) (Fig.18.1, no. 9).

2. S. eriophora Bornm. in Notizbl. Bot. Gart. Berlin 14: 282 (1938).

I have not seen material of this species. From descriptions it appears to differ markedly from S. calycina by its dense indumentum, its purple corolla and by the fact that all 4 nutlets seem to mature.

27.3 MORPHOLOGY AND RELATIONSHIPS

The two species appear to share many characters in common and form a very natural genus. They seem to differ principally by indumentum and form of the calyx.

The shortly infundibular corollas with small scales closely resemble those of some species of Paracynoglossum and are in marked contrast to the

larger corollas of Trichodesma and most species of Caccinia. The anthers are also typically Cynoglossum-type in morphology and insertion, being neither exserted nor appendaged as in Caccinia, Heliocarya and Trichodesma.

The gynobase and accrescent calyx (Fig. 18.1, no. 8) are similar to those of the tribe Trichodesmeae; in particular, the four vertical crests on the gynobase, which alternate with the nutlets, seem to indicate a relationship. However, similar crests with alternating deep depressions also occur in Ivanjohnstonia jaunsariensis of the Cynoglosseae, and, as in Suchtelenia, are correlated with a very strongly accrescent calyx and bracteate cymes. Ivanjohnstonia differs from Suchtelenia (at least from S. calycina) in the fact that all four nutlets mature, and by its perennial life form.

The facts suggest that the tribe Trichodesmeae as delimited by ZAKIROV (1941) is a rather unnatural assemblage of genera brought together by weighting the calyx and gynobase characters. Trichodesma itself (formerly classified in the Cynoglosseae, along with Heliocarya and Caccinia) bears a strong resemblance to Borago (tribe Boragineae) although this probably represents convergence. Both genera, along with Trachystemon (a close ally of Borago) are characterised by drooping flowers with their anthers exserted and (in Borago and Trichodesma) connivent in a cone. Differences in nutlet attachment, however, have led (justifiably) to their classification in different tribes - Borago and Trachystemon have the nutlets attached basally to a flat gynobase, while in Trichodesma they are ventrally attached to a pyramidal gynobase.

Caccinia and Heliocarya are very closely related, sharing a zygomorphic long-tubed corolla with acute lobes and a single fertile anther. They seem rather distantly related to Trichodesma and even less to Suchtelenia.

27.4 PALYNOLOGY

The pollen of Suchtelenia has been studied by AVETISIAN (1956) and BARBIER & MATHEZ (1973). Avetisian's study was particularly detailed, all Russian races of S. calycina having been examined. Both he and Barbier & Mathez questioned the relationships of Suchtelenia with Caccinia and Trichodesma. As I was unable to obtain usable flowers of Suchtelenia calycina (all sheets I examined were in fruit with only a few old flowers which had shed their pollen), the description below is based on Avetisian's results and illustrations. The pollen of S. eriophora is unknown,

27.4.1 Description:

Pollen elliptic, without equatorial constriction (when acetolysed), heterocolpate, tricolporate, tripseudocolpate. Amb hexagonal, sides bearing colpi slightly emarginate, sides bearing pseudocolpi ± straight. P (acetolysed) = 14-15 μm, E (acetolysed) = 8.4-9.8 μm. P/E = 1.57-1.86 (prolate). Colpi narrowly rhombic, 9.8-12.6 x 1.2-1.5 μm. Endoaperture a lalongate endocolpus. Pseudocolpi ± linear. Collar apparently present but very slender.

27.4.2 Discussion:

BARBIER & MATHEZ (1973) included S. calycina in their group C (dumb-bell shaped pollen). The discrepancy between this observation and Avetisian's is no doubt due to technique - acetolysis seems to distort Boraginaceae pollen in unpredictable ways.

As observed by Avetisian, the pollen is similar to that of Ivanjohnstonia and some Paracynoglossum, while Barbier & Mathez's data relate it still more to Paracynoglossum. In size and morphology it is quite different to the large ± spheroidal grains (c. 21 x 20-21 μm) of both Caccinia and Trichodesma. Moreover, the sexine is ± smooth or only finely patterned, not distinctly sculptured as in those genera, and the grains are heterocolpate with both colpi and pseudocolpi (in Caccinia and

Trichodesma, only 3 true apertures are present). These are fundamental differences in pollen morphology, which suggest that the correct alignment of *Suchtelenia* is not in the *Trichodesmeae* but in the *Cynoglosseae*.

CHAPTER 28

EXCLUDED GENERA

As mentioned in sect. 1.4, five genera usually included in the Cynoglosseae are here excluded, three for the first time. These are Actinocarya Bentham, Antiotrema Hand.-Mazz., Embadium Black, Pectocarya DC., and Thyrocarpus Hance.

28.1 ACTINOCARYA Bentham:

Actinocarya is a ditypic Himalayan genus. Treatments include those by JOHNSTON (1924b) and KAZMI (1971). BRAND (1921) removed this genus to the Lithospermeae, but Johnston (op. cit.) re-instated it as a member of Cynoglosseae and the few later workers have followed him. It belongs to the obscurely defined circle of genera centred on Lepechiniella (Eritrichieae) and Omphalodes (Cynoglosseae). On balance, it seems best to classify it in Eritrichieae on the basis of its nutlet attachment, which is not truly apical as in Cynoglosseae, and its greater similarity to genera of the Eritrichieae such as Stephanocaryum M. Popov and Lepechiniella.

28.2 ANTIOTREMA Hand.-Mazz.:

Antiotrema is a monotypic genus endemic to Yunnan (S.W. China). Its species, A. dunnianum (Diels) Hand.-Mazz. (Syn: Henryetta mirabilis Brand) is a tall herb with villous leaves and stems and relatively large reddish blue or reddish-black flowers. In habit and floral morphology there is a strong resemblance to the sympatric species Eleutherostylum triste (Diels) R. Mill of the Cynoglosseae (cf. sect. 11.6). The pollen of the two species is also rather similar. However, A. dunnianum has small brown rugulose inverted nutlets which are shorter than and included in the calyx, while those of E. triste are much larger, exceeding the calyx, apically attached to the gynobase, and glochidiate as in Lindelofia and Cynoglossum.

The nutlet attachment in Antiotrema is apparently basal, but actually the nutlets are inverted in a similar fashion to those of Bothriospermum. This led BRAND (1929) to classify his new genus Henryetta in the Lithospermeae.

Bothriospermum itself has had a chequered taxonomic history. First placed in Anchuseae by ENDLICHER (1839), it was removed to Lithospermeae by DE CANDOLLE (1846) and transferred to Eritrichieae by BENTHAM & HOOKER (1876). BRAND (1931) followed De Candolle, but JOHNSTON (1924b) considered it to belong to Cynoglosseae. POPOV (1953) awarded it subtribal rank within Lithospermeae, but in his index this was wrongly indicated as 'Tribe Bothriospermeae'. RIEDL (1967) transferred Popov's subtribe Bothriospermeae to his new tribe Trigonotideae. I am inclined to recognise the Bothriospermeae as a tribe in its own right (following Popov's index); when Antiotrema and Thyrocarpus (28.3) are added, it forms a distinct unit which can be delimited from the Trigonotideae by its inverted nutlets. The necessary change in rank is made below.

Tribus Bothriospermeae (M. Popov) R. Mill, stat. nov. Syn: Tribus Lithospermeae Gürke subtribus Bothriospermeae M. Popov in Fl. URSS 19: 235 (1953) ('tribus Bothriospermeae M. Popov, op. cit. 720 in indice); Tribus Trigonotideae (M. Popov) H. Riedl in Rech. fil., Fl. Iranica - Boraginaceae 56 (1967) p.p.

Type genus: Bothriospermum Bunge. Constituent genera: Bothriospermum Bunge, Antiotrema (Diels) Hand.-Mazz., Thyrocarpus Hance.

28.3 THYROCARPUS Hance:

The Chinese genus Thyrocarpus has also traditionally been treated as a member of Cynoglosseae. Its rimmed nutlets have been used to relate the genus to Omphalodes sensu lato (including the three Japanese species here segregated as the genus Desmolopha: Chapter 25). Morphologically, it shows vegetative resemblance to Desmolopha. The nutlet attachment,

however, aligns the genus with Bothriospermum, as was noted by GUŞULEAC (1927c) and RIEDL (1968). In the present thesis I exclude it from Cynoglosseae and consider it to belong to Bothriospermeae.

28.4 PECTOCARYA DC.:

Pectocarya is a difficult genus of about twelve species extending from California down the western seaboard of N. America to Mexico and western S. America as far South as Chile. Its species are all highly derived annuals and very closely related; the several accounts of the genus do not agree as to specific limits or indeed to the total number of species in the genus.

The genus, however, is much more easily defined. All species have a dense hard white-setose indumentum, very small (c. 1 mm) white flowers with a rather long cylindrical tube and minute subpatent limb; the anthers are set well down near the base of the tube. The nutlets are very derived, and frequently reduced to 2. They are linear to obovate, usually paired and divaricate, with a thin wing-like margin which bears a fringe of uncinate hairs. Nutlets are essential for the identification of the species.

Pectocarya has apparently always been classified in Cynoglosseae. There has been no formal re-assessment of its taxonomic position since JOHNSTON (1924a), who considered it to be the most derived genus of the tribe. It is probable that recent authors have merely followed Johnston (the acknowledged authority on Boraginaceae in his day) without subjecting his views to critical examination.

It is extremely difficult to accommodate Pectocarya in the Cynoglosseae as here delimited. While its nutlet attachment seems to be of the Cynoglosseae type, this is the only character in which it resembles the other genera of that tribe. If grouped in Cynoglosseae, it would be unique in its floral morphology, palynology and nutlet structure. Several genera of Eritrichieae, however, display very similar combinations of characters,

notably Lappula, Harpagonella and Embadium (see sect. 28.5). Harpagonella in particular shows a very strong affinity to Pectocarya and like it was classified in Cynoglosseae by JOHNSTON (1924a) follows Bentham & Hooker. Other workers, however, have followed GÜRKE (1895) in recognising the monotypic tribe Harpagonelleae on account of the very peculiar development of the calyx and nutlets to form a dispersal unit. In my opinion, this merely represents an extension of trends begun in Pectocarya and the recognition of Tribe Harpagonelleae obscures the close natural relationships between the two genera, which are sympatric in Baja California. Both have a similar floral morphology to Cryptantha and some species of Lappula, two undisputed members of Eritrichieae, and they may represent highly evolved desertic derivatives. Therefore I classify both Pectocarya and Harpagonella in the Tribe Eritrichieae. Such a classification was in fact implied although not proposed by SHREVE & WIGGINS (1964), in their account of the flora of the Sonora Desert (Mexico), by placing Pectocarya next to Lappula in the sequence of genera.

28.5 EMBADIUM Black:

Embadium is a tritypic Australian genus first described by BLACK (1931) and recently treated by ISING (1965). Neither he nor JOHNSTON (in litts.) managed to satisfactorily resolve the tribal placing of the genus. Johnston was uncertain as to whether it belonged to Cynoglosseae (near Omphalodes) or to Eritrichieae (near Lappula). In his first letter to Black, Johnston tentatively referred it to Cynoglosseae. He drew attention to the medial nutlet attachment, which resembled that of Hackelia and Eritrichium (Eritrichieae) but pointed out that in all other positive characters it 'fits into (Cynoglosseae) best, and close to Omphalodes', and stated that he believed that 'the strict and sole use of nutlet attachment in defining the tribes of the Borages leads to unnaturalness in classification' -

a view which I support. He maintained a similar opinion in his second letter, but in his third (sent to Ising: dated 16 ix 1954, published in ISING 1965, p. 284) he showed a marked change of mind, being convinced 'that it is most closely related to Lappula'. Ising himself did not commit himself to a final tribal placing of Embadium.

Its species are hispid annual herbs with minute white flowers very similar to those of Pectocarya, and with somewhat similar ecological preferences, being adapted to the very dry habitats of the salt deserts in the interior of South Australia. Omphalodes (Cynoglosseae) and Embadium only converge in superficial nutlet characters; otherwise they are totally distinct, the details of nutlet structure and embryology confirming the lack of natural relationship. Palynological work done by Johnston and myself also supports the view that they are not closely allied. The nearest relative in Australia, albeit a distant one, appears to be the allopatric monotypic genus Omphalolappula Brand, which is sometimes included in Lappula (cf. POPOV 1953). Embadium and Omphalolappula agree in nutlet attachment, bracteate cymes and in their general facies. There is little apparent close relationship between Embadium and true Lappula, however, nor is there any relationship below tribal level with either Eritrichium or Hackelia. The evidence suggests that Embadium should be assigned to the Eritrichieae. The median nutlet attachment is typical of that tribe and unlike the ± apical attachment prevalent in the Cynoglosseae. Within the Eritrichieae it is unquestionably a very distinct and derived genus possibly related to (or convergent with) Pectocarya and Harpagonella.

BIBLIOGRAPHY

(*Denotes references not seen in original)

AGNEW, A.D.Q. 1974.
Upland Kenya Wild Flowers. A Flora of the Ferns and Herbaceous Flowering Plants of Upland Kenya. London: Oxford University Press.

*AHUJA, M.P. 1955.
Chromosome numbers of some plants.
Ind. J. Gen. & Pl. Br. 15: 142-143.

*AHUJA, M.H. & NATARAJAN, A.T. 1957.
Chromosome number of some common plants.
Curr. Sci. 26: 117.

*AKRAMOV, S.T. 1968.
Chem. Abstr. 68: 47001-v.

*AKRAMOV, S.T., KITATMITDINOVA, F. & YUNUSOV, S.Y. 1962.
Chem. Abstr. 57: 16676-b.

*AKRAMOV, S.T., KITATMITDINOVA, F. & YUNUSOV, S.Y. 1964a.
Chem. Abstr. 61: 4700-c.

*AKRAMOV, S.T., KITATMITDINOVA, F. & YUNUSOV, S.Y. 1964b.
Chem. Abstr. 61: 11005e.

*AKRAMOV, S.T., KITATMITDINOVA, F. & YUNUSOV, S.Y. 1965.
Chem. Abstr. 63: 16770-e.

ALDÉN, B. 1976.
Floristic reports from the high mountains of Pindhos, Greece.
Bot. Not. 129: 297-321.

ARYAVAND, A. 1976.
Contribution à l'étude cytotaxinomique de quelques Angiospermes de l'Iran.
Bot. Not. 128: 299-311. (1975 - distributed 9 ii 1976).

ARYAVAND, A. 1977.
In LÖVE, A. (ed.), IOPB Chromosome number reports LVII.
Taxon 26: 443-444.

AVETISIAN, E.M. 1956.
Morphologiya Mikrospory Byorazhinikovich (Pollen morphology of the Boraginaceae).
Trudy Bot. Inst. Akad. Armen. SSSR 10: 7-66.

BAKER, J. & WRIGHT, C.H. 1906.
Borageineae. In Thiselton-Dyer, W.J., Flora of Tropical Africa vol. 4 (2).

BALDACCI, A. 1899.
Rivista della collezione botanica fatta nel in 1896 in Albania.
Nuovo Gior. Bot. Ital. n.s. 6(4): 333-356.

*BANDYUKOVA, V.A. & FVANESOV, E.T. 1971.
O veroyatnosh obnanuzheniya flavanov, flavanonov, isoflavonoidov v nekatorykti semeistvakh vysshikh rastenii. (On the probability of finding flavones, flavanones and isoflavonoids in certain families of higher plants, I.).
Rast. Resur. 7(3): 321-328.

BARBIER, E. & MATHEZ, J. 1973.
Contribution à l'étude des Cynoglossées (Boraginacées): Pardoglossum, genre nouveau du Bassin mediterranéen occidental.
Candollea 28: 281-323.

BASLER, A. 1972.
Cytotaxonomische Untersuchungen an der Boraginaceen-Gattung Symphytum L.: Untersuchungen an überwiegend norddeutschen Pflanzen der Arten S. asperum Lepech., S. officinale L. und S. x uplandicum Nym.
Bot. Jahrb. 92: 508-533.

BELL, C.R. 1965.
Documented chromosome numbers of plants 65: 3.
Sida 2: 168-170.

BENTHAM, G. 1869.
Flora Australiensis vol. 4: Stylidieae - Pedalineae. London: L. Reeve & Co.

BENTHAM, G. & HOOKER, J.D. 1876.
Genera Plantarum. London: L. Reeve & Co.

BLACK, J.M. 1931.
Additions to the flora of South Australia, 29.
Trans. & Proc. Roy. Soc. S. Australia 55: 136-142.

BLAISE, S. 1972.
Problèmes taxonomiques posés par l'homogenéité apparente du genre Myosotis.
Candollea 27: 65-81.

BOISSIER, E.P. 1843-1856.
Diagnoses plantarum orientalium novarum e familiis thalamifloris.
Genève, Leipzig, Paris & Como: Ramboz.
(Paracaryum is described in series 1, part 11, 1849).

BOISSIER, E.P. 1875.
Flora Orientalis vol. 4. Genève & Basel: H. Georg.

BOLKHOVSHIKH, Z., GRIF, V., MATVEJEVA, T. & ZAKHARYEVA, O. 1969.
Chromosome numbers of flowering plants. Leningrad: Acad. Sci. USSR., V.L. Komarov Botanical Institute.

BOLUS, H. 1890.
Tysonia africana, Bolus.
Hooker's Ic. Pl. 20: t. 1942.

BORNMÜLLER, J. 1907.
Beiträge zur Flora Elbursgebirge Nord-Persiens.
Bull. Herb. Boiss. 9: 773-788.

BORNMÜLLER, J. 1914.
Über eine neue Solenanthus-Art aus den Balkan.
Feddes Rep. 12: 276-279.

BORNMÜLLER, J. & GAUBA, E. 1942.
Florae Keredjensis fundamenta (Plantae Caubacanae Iranicae).
Supplementum, 2. Enumeratio specierum.
Feddes Rep. 51: 209-239.

BRAMWELL, D. 1978.
Boraginaceae. In HEYWOOD, V.H. (ed.), Flowering Plants of the World.
Oxford: University Press.

BRAND, A. 1915.
Neue Gattungen und Arten der Cynoglosseae.
Feddes Rep. 13: 545-550.

BRAND, A. 1921.
Borraginaceae-Borraginoideae-Cynoglosseae.
In A. Engler, Das Pflanzenreich Heft 78 (IV. 252).

BRAND, A. 1929.
Decas specierum novarum nona.
Feddes Rep. 26: 168-172.

BRAND, A. 1931.
Borraginaceae-Borraginoideae-Cryptantheae.
In A. Engler, Das Pflanzenreich Heft 97 (IV. 252).

BRAUN-BLANQUET, J. & MAIRE, R. 1922.
Contributions à l'étude de la flore marocaine.
Bull. Soc. Hist. Nat. Afrique Nord 13 (fasc. 1): 13-22.

BRECKLE, S.W. 1971.
Vegetation in Alpine Regions of Afghanistan.
In DAVIS, HARPER & HEDGE (eds.), Plant life of South West Asia 107-116.
Botanical Society of Edinburgh/Aberdeen University Press.

BRECKLE, S.W. 1974.
Notes on alpine and nival flora of the Hindu Khush, East Afghanistan.
Bot. Not. 127: 278-284.

BREWBAKER, J.L. 1957.
Pollen cytology and self incompatibility systems in plants.
J. Heredity 48: 271-277.

BRIDGES, Susan 1969.
(Chromosome number report for Heliotropium indicum L.)
In LÖVE, A.(ed.), IOPB Chromosome Number Rept. 22. Taxon 18: 433.

BRITTON, D.M. 1951.
Cytogenetic Studies on the Boraginaceae.
Brittonia 7: 233-256.

BRONCKERS, F. 1968.
Les Nomenclatures en Palynologie.
Bull. Soc. Roy. Bot. Belg. 101: 23-35.

BROWN, R. 1810.
Prodromus Florae Novae Hollandiae et Insulae Van Diemen.
London: J. Johnson & Sons.

*CABALLERO, A. 1945.
Ilustraciones de la flora endémica española.
Anal. Jard. Bot. Madrid 5: 523-557.

CAMP, W.H. 1940.
The concept of the genus. 5. Our changing generic concepts.
Bull. Torrey Bot. Club 67: 381-389.

De CANDOLLE, A. 1839.
Boragineae. In MEISNER, C.F., *Plantarum vascularium genera secundum ordines naturales digesta eorumque differentiae et affinitatis tabulis diagnosticis expositae.* vol. 1. Lipsiae: Weidmann.

De CANDOLLE, A. 1846.
Prodromus systematis naturalis regni vegetabilis ... Vol. 10. Paris.

CASASECA, B. & FERNANDEZ DIEZ, J. 1976.
Omphalodes pavoniana Boiss., Planta Española.
Lagascalia 6: 247-249.

CHISAKI, H.F. 1959.
In: Documented chromosome numbers of plants.
Madroño 15: 50.

CLAPHAM, A.R., TUTIN, T.G. & WARBURG, E.F. 1962.
Flora of the British Isles, ed. 2. Cambridge: University Press.

CLARKE, C.B. 1883.
Boragineae. In HOOKER, J.D. fil., *The Flora of British India* vol. 4, part 10: pp. 134-180. London: Secretary of State for India.

CLARKE, G.C.S. 1977.
The Northwest European Pollen Flora, 10. Boraginaceae.
Rev. Palyn. Palaeobot. 24: 59-101.

CONSTANCE, L. 1951.
The Versatile Taxonomist.
Brittonia 7: 225-231.

CONSTANCE, L. 1964.
Systematic botany - an unending synthesis.
Taxon 13: 259-273.

COOKE, T. 1905.
Flora of the Presidency of Bombay. vol. 2: Compositae-Gramineae.
London: Taylor & Francis.

COSSON, E. S.-C. 1856.
Note sur quelques espèces nouvelles d'Algerie.
Bull. Soc. Bot. Fr. 3: 704-709.

COSSON, E. S.-C. 1897.
Illustrationes florae atlanticae. Vol. 2/7. Paris.

COULTER, J.M. & CHAMBERLAIN , C.J. 1904.
Morphology of Angiosperms. New York: D. Appleton & Co.

CRÉTÉ, M.P. 1955.
Embryogénie des Boraginacées. Développement de l'embryo chez Cynoglossum officinale.
Compt. Rend. Acad. Sci. Paris 241: 660-662.

CRONQUIST, A. 1968.
The Evolution and Classification of Flowering Plants. London: Nelson (Riverside Studies in Biology).

*CROWLEY, H.C. & CULVENOR, C.C.J. 1962.
Austr. J. Chem. 15: 139.

CULVENOR, C.C.J. 1978.
Pyrrolizidine alkaloids - occurrence and systematic importance in angiosperms.
Bot. Not. 131: 473-486.

*CULVENOR, C.C.J. & SMITH, C.W. 1967.
Austr. J. Chem. 20: 2499.

CZERAPANOV, S.K. 1973.
Additamenta et Corrigenda ad 'Floram URSS' (tomi I-XXX). Leningrad.

DAHLGREN, R. 1977.
A commentary on a diagrammatic presentation of the Angiosperms in relation to the distribution of character states. Pl. Syst. Evol. Suppl. 1:253-283.

DANDY, J.C. & STEARN, W.T. 1961.
What is Cynoglossum lusitanicum L.?
Agron. Lusit. 23: 8-17.

DAVIS, Gwenda L. 1966.
Systematic Embryology of the Angiosperms. New York: John Wiley & Sons.

DAVIS, P.H. 1951.
Cliff vegetation in the Eastern Mediterranean.
J. Ecol. 39: 63-93.

DAVIS, P.H. 1956.
Fourteen new species from Turkey.
Notes R.B.G. Edinb. 22: 65-84.

DAVIS, P.H. 1971.
Distribution patterns in Anatolia with particular reference to endemism.
In DAVIS, HARPER & HEDGE (eds.), Plant Life of South West Asia, 15-27.
Botanical Society of Edinburgh/Aberdeen University Press.

DAVIS, P.H. 1978.
The moving staircase: a discussion on taxonomic rank and affinity.
Notes R.B.G. Edinb. 36: 325-340.

DAVIS, P.H. (ed.) 1979 ('1978').
Flora of Turkey and the East Aegean Islands, 6. Edinburgh: University Press.

DAVIS, P.H. & HEDGE, I.C. 1971.
Floristic links between Northwest Africa and Southwest Asia.
Ann. Naturh. Mus. Wien 75: 43-57.

DEGEN, A. von 1903.
Über zwei neue Solenanthus-Arten in Europa.
Mag. Bot. Lap. 2: 311-318.

*DELAY, J. 1970.
Orophytes.
Inf. Ann. Caryosyst. et Cytogenet. 4: 1-16.

*DERSCH, G. 1968.
Über einige Chromosomenzahlungen an mitteleuropaischen Blutenpflanzen.
Abh. Ver. Naturk. 52: 9-12.

DIELS, L. 1912.
Plantae Chinenses Forrestianae. New and Imperfectly Known Species.
Notes R.B.G. Edinb. 5: 161-304.

*DIERS, L. 1961.
Der Arteil an Polyploiden in den Vegetationsgüsteln der Westkordillera Perus.
Zeitschr. Bot. 49: 437-488.

DING, H. 1950. Cited (as HOU, D.) on p. 736. (q.v.).

DRUCE, G.C. 1913.
Notes on Nomenclature, part 2. The Abridgement of Miller's Gardener's Dictionary of 1754.
Rep. Bot. Exch. Club Brit. Isles, Suppl. 3: 426-436.

DYER, 1975. See foot of page.

EASTWOOD, Alice 1896.
Descriptions of some new species of Californian plants.
Proc. Calif. Acad. Sci. ser. 2, 6: 422-430 + Tabs. LIII-LIX.

EDGAR, J.A., CULVENOR, C.C.J. & PLISKE, T.E. 1974.
Coevolution of Danaid butterflies with their host plants.
Nature (London) 250: 646-648.

EDMONDSON, J.R. 1977.
Omphalodes in DAVIS, P.H. (ed.), Materials for a Flora of Turkey XXXIV.
Notes R.B.G. Edinb. 35: 300-302.

ENDLICHER, S.L. 1839.
Genera plantarum secundum ordines naturales disposita. Vindobonae (Wien): Fr. Beck.

ERDTMAN, G. 1943.
Introduction to pollen analysis. Waltham, Massachusetts: Chronica Botanica Co.

*ERDTMAN, G. 1948.
Did Dicotyledonous plants exist in early Jurassic times?
Geol. Foren. Stockh. Forh. 70.

ERDTMAN, G. 1952.
Pollen morphology and plant taxonomy. Stockholm: Almqvist & Wiksell.

DYER, R.A. 1975.
The genera of Southern African flowering plants. Pretoria.
Dept. of Agric. Techn. Services, Botanical Research Institute,
vol. 1 - Dicotyledons.

ERDTMAN, G. 1960a.
Pollen walls and angiosperm phylogeny.
Bot. Not. 113: 41-48.

ERDTMAN, G. 1960b.
Notes on the finer structure of some pollen grains.
Bot. Not. 113: 285-288.

ERDTMAN, G. 1963.
Palynology.
Adv. Bot. Res. 1: 149-208.

ERDTMAN, G. 1964.
Ein Beitrag zur Kenntnis der Pollenmorphologie von Lactoris fernandeziana und Drimys winteri.
Grana Palynol. 5: 33-38.

ERDTMAN, G. 1966a.
À propos de la stratigraphie de l'exine.
Pollen et Spores 8: 5-7.

ERDTMAN, G. 1966b.
Pollen Morphology and Plant Taxonomy: Angiosperms. New York: Hafner (with addendum).

ERDTMAN, G. 1968.
On the exine in Stellaria crassipes Hult.
Grana Palynol. 8: 271-276.

ERDTMAN, G. 1969.
Handbook of palynology. New York: Hafner.

ERDTMAN, G. 1972.
Pollen Morphology and Plant Taxonomy: Angiosperms. (Reprint with addendum). New York: Hafner.

EYDE, R.H. 1972.
Pollen of Alangium: toward a more satisfactory synthesis.
Taxon 21: 471-477.

FAEGRI, K. 1956.
Recent trends in palynology.
Bot. Rev. 22: 639-664.

FAIRBROTHERS, D.E., MABRY, T.J., SCOGIN, R.L. & TURNER, B.L. 1976 ('1975').
The Bases of Angiosperm Phylogeny: Chemotaxonomy.
Ann. Missouri Bot. Gard. 62: 765-800.

*FARUQI, S.A. 1961a.
A cytological note on Heliotropium angiospermum Murray.
Southwest Nat. 6: 100.

FARUQI, S.A. 1961b.
Cytological studies in Heliotropium from West Pakistan.
Caryologia 14: 313-318.

FATHIMA KHALEEL, Tasneem 1974.
Embryology of Cynoglossum denticulatum DC.
Bot. Not. 127: 193-210.

FAVARGER, C. & CONTANDRIOPOULOS, J. 1961.
Essai sur l'endémisme.
Bull. Soc. Bot. Suisse 71: 384-408.

FEDTSCHENKO, B. 1913.
Perech. Rast. Turk. 5: 65, no. 3127.

FERNANDES, A. & LEITÃO, Maria Teresa 1972.
Contribution à la connaissance cytotaxinomique des Spermatophyta du Portugal: V. Boraginaceae.
Bol. Soc. Brot. 46: 389-405.

FIORI, A. & PAOLETTI, G. 1902.
Flora Analitica d'Italia. Vol. 2. Padova.

FISCHER, F.E.L. von & MEYER, C.A. von 1842.
Enumeratio (prima et alter) plantarum novarum a cl. Schrenk lectarum.
Petropoli.

FRANCHET, A. 1888.
Plantae Davidianae ex Sinarum imperio. Deuxième partie: Plantes du Thibet Oriental (Province de Moupine). Paris: G. Masson.

FRANCHET, A. & SAVATIER, L. 1875 & 1879.
Enumeratio Plantarum in Japonia sponte crescentium. Pars I: 1875.
Pars II: 1879.

*Di FULVIO, Teresa E. 1969.
Recuentos cromosomicos en Heliotropium (Boraginaceae).
Kurtziana 5: 89-94.

GADELLA, T.W.J. & KLIPHUIS, E. 1966.
Chromosome numbers of flowering plants in the Netherlands 2.
Proc. Roy. Neth. Acad. Sci. ser. C, 69: 541-556.

GADELLA, T.W.J. & KLIPHUIS, E. 1969.
Cytotaxonomic studies in the genus Symphytum 2. Crossing experiments between Symphytum officinale L. and Symphytum asperum Lepech.
Acta Bot. Neerl. 18: 544-549.

GENTRY, J.L. & CARR, R.L. 1976.
A revision of the genus Hackelia (Boraginaceae) in North America, North of Mexico.
Mem. New York Bot. Gard. 26: 121-227.

GIBBS, R.D. 1974.
Chemotaxonomy of flowering plants. New York: McGraw Hill/Queen's University Press.

GOEBEL, K. 1887. (Transl. H.F. GARNSEY; rev. I.B. BALFOUR)
Outlines of classification and special morphology. Oxford: Clarendon Press.

*GORSHKOVA, A.A., KOPYTOVA, L.D. & SPIVAK, A.I. 1969.
Vliyanie nedostatochnogo i vlazhneniya i ponizhennykh temperatur stepnogo Zabaikal'- ya na morfo-fiziologicheskie svoistva travyanistykh rastenii (The effect of the inadequate moisture and low temperature of the Transbaikal steppes on the morphophysiological properties of herbaceous plants).
Izv. Biol.-Geogr. Nauch-Issled. Inst. Irkutsk Univ. 23: 67-79 (transl. from Ref. Zh. Biol. 1970, no. 6V321).

GRANT, V. 1971.
Plant Speciation. New York & London: Columbia University Press.

GRAU, J. 1967.
Primäre und Sekundäre Chromosomenbasiszahlen bei Omphalodes.
Öst. Bot. Zeitschr. 114: 66-72.

GRAY, A. 1885.
A revision of some boraginaceous genera.
Proc. Amer. Acad. Arts & Sci. 20: 257-259 & 262-264.

GREENMAN, J.M. 1904.
Contributions from the Gray Herbarium of Harvard University n.s. 28: 5.
Diagnoses and synonymy of Mexican and Central American Spermatophytes.
Proc. Amer. Acad. Arts & Sci. 40: 28-52.

GREENMAN, J.M. 1905.
Descriptions of spermatophytes from the southwestern United States, Mexico and Central America.
Proc. Amer. Acad. Arts & Sci. 41: 235-278.

GUEGUEN, F. 1903.
Anatomie comparée du tissu conducteur du style et du stigmate des phanerogames.
J. Bot. (Paris) 16: 15-30, 48-65, 138-144, 167-180, 300-313.

GÜRKE, M. 1893-1895.
Borraginaceae. In Engler, H.G.A. & Prantl, K.A.E., Die Natürlichen Pflanzenfamilien 4 (3a): 71-131.

GUSTAVSSON, L.-Å. 1978.
Floristic reports from the high mountains of Sterea Ellas, Greece. 1.
Bot. Not. 131: 7-25.

GUŞULEAC, M. 1927a.
Die europäischen Arten der Gattung Anchusa Linné.
Bul. Fac. Ştiinţe Cernăuţi 1: 73-123.

GUŞULEAC, M. 1927b.
Die aussereuropäischen Arten der Gattung Anchusa Linné.
Bul. Fac. Ştiinţe Cernăuţi 1: 235-325.

GUŞULEAC, M. 1927c.
Zur Anatomie und Biologie der Bothriospermum und Thyrocarpusfrüchte.
Beih. Bot. Centr. 43: 255-266.

GUŞULEAC, M. 1928a.
Die monotypischen und artenarmen Gattungen der Anchuseae (Caryolopha, Brunnera, Hormuzakia, Gastrocotyle, Phyllocara, Trachystemon, Procopiana und Borago).
Bul. Fac. Ştiinţe Cernăuţi 2: 394-461.

*GUŞULEAC, M. 1928b.
Sistemul Boragineelor in lumina cercetărilor noui.
Intâiul Congr. Nat. Naturalist. România 1: 183-197.

GUŞULEAC, M. 1929a.
Species Anchusae generis Linn. hucusque cognitae.
Feddes Rep. 26: 286-322.

GUŞULEAC, M. 1929b.
Hormuzakia und Phyllocara, zwei neue Anchuseegattungen.
Feddes Rep. 26: 337-338.

GVINIASHVILI, T.N. 1972.
Nekotorye dannye po kariologii kavkazshikh vidov Symphytum L. v svyazi s ikh sistematikoi (Some data on the karyology of Caucasian species of Symphytum L. with respect to their taxonomy).
Bot. Zh. 57: 1120-1126.

HALL, H.M. & CLEMENTS, F.C. 1923.
The phylogenetic method in taxonomy.
Carnegie Institute of Washington Publication No. 326: 1-30.

HANDEL-MAZZETTI, H. F. von 1920.
Plantae Novae Sinenses 7.
Anz. Akad. Wiss. Wien.

HARA, H. 1972.
Corresponding taxa in North America, Japan and the Himalayas.
In VALENTINE, D.H. (ed.), Taxonomy, Phytogeography and Evolution 61-72.
London & New York: Academic Press.

HARMATA, Krystyna 1977.
Pollen morphology and taxonomy in the genera Symphytum L. and Procopiana Guşuleac.
Prace Botaniczne (Zeszyty Nauk. Univ. Jagiellońskiego 459) 5: 7-29.

HEDBERG, Inga & HEDBERG, O. 1977.
Chromosome numbers of afroalpine and afromontane angiosperms.
Bot. Not. 130: 1-24.

HEDGE, I.C. 1976.
A systematic and geographical survey of the Old World Cruciferae.
In VAUGHAN, MACLEOD & JONES (eds.), The biology and chemistry of the Cruciferae 1-45. London & New York: Academic Press.

HEDGE, I.C. & WENDELBO, P. 1970
Some remarks on endemism in Afghanistan.
Israel J. Bot. 19: 401-417.

HEGNAUER, R. 1964.
Chemotaxonomie der Pflanzen 3.

HEGNAUER, R. 1966.
Comparative Phytochemistry of Alkaloids.
In SWAIN, T. (ed.) Comparative Phytochemistry 211-230.
London/New York: Academic Press.

HENRY, T.A. 1949.
The Plant Alkaloids, ed. 4. New York: Blaikston Co.

HICKEY, L.J. & WOLFE, J.A. 1976 ('1975').
The Bases of Angiosperm Phylogeny: Vegetative Morphology.
Ann. Missouri Bot. Gard. 62: 538-589.

HIGGINS, L.C. 1976a.
Two new species from the Chihuahuan desert.
Phytologia 33: 411-413.

HIGGINS, L.C. 1976b.
A new name for Cynoglossum erectum (Boraginaceae).
Phytologia 34: 234.

HITCHCOCK, C.L. & CRONQUIST, A. 1973.
Flora of the Pacific Northwest: an illustrated manual. Seattle & London: University of Washington Press.

HITCHCOCK, C.L., CRONQUIST, A., OWNBEY, Marion & THOMPSON, J.W. 1959.
Vascular plants of the Pacific Northwest. Part 4: Ericaceae through Campanulaceae. Seattle & London: University of Washington Press.

HOHENACKER, R. Fr., 1838.
Enumeratio plantarum quas in itinere per provinciam Talych collegit R. F. Hohenacker simul cum additamentis et emendationibus ad 'Enumerationem plantarum territorii Elisabethpolensis et provinciam Karabach' receptam.
Bull. Soc. Imp. Nat. Moscou 1838 (3): 239-332.

HOOKER, J.D. & THOMSON, T. 1855.
Flora Indica. London: W. Pamplin.

HOOPER, P.T. 1978.
Pyrrolizidine alkaloid poisoning: pathology with particular reference to differences in animal and plant species.
In KEGLER, R.F., van KAMPEN, K.R. & JAMES, Lynn F., Effects of Poisonous Plants on Livestock pp. 161-174. New York, San Francisco & London: Academic Press.

HOU, D. 1950.
The Boraginaceae of Taiwan.
Taiwania 1: 223-268.

HUANG, Tseng-Chieng 1972.
Pollen flora of Taiwan. Taipei: National Taiwan University, Botany Department Press.

HUMMEL, K. & STAESCHE, Karin 1962.
Die Verbreitung der Haartypen in natürlichen Verwandtschaftsgruppen.
Handb. der Pflanzenanatomie 4(5): 209-288.

HUTCHINSON, J. 1973.
Evolution and Phylogeny of Flowering Plants. Oxford: University Press.

HUYNH, Kim-Lang 1971.
Le pollen du genre Arnebia Forssk. et du genre Macrotomia DC. (Boraginaceae) et la position taxonomique particulière du M. echioides (L.) Boiss.
Candollea 26: 165-171.

INAMDAR, J.A. & PATEL, R.C. 1973.
Structure, ontogeny and classification of trichomes in some Polemoniales.
Feddes Rep. 83: 473-488.

INGRAM, J. 1960.
Studies in the cultivated Boraginaceae 3. Omphalodes.
Baileya 8: 137-141.

ISING, E.H. 1965.
Two new species of Embadium (Boraginaceae).
Trans. Roy. Soc. South Australia 89: 283-289.

*ISMAILOV, N.M. 1972.
Rasprodelenie alkaloidonosnykh rastenii Azerbaidzhana po ekologicheskim gruppam i zhiznennykh formam (Distribution of alkaloid bearing plants of Azerbaijan according to ecological groups and life forms).
Rast. Resur. 8: 176-180.

*ISMAILOV, N.M. 1973.
Geograficheskoe raspredelenie alkaloidonosnykh rastenii flory Azerbaidzhana (Geographic distribution of alkaloid bearing plants of Azerbaijan).
Rast. Resur. 9: 11-18.

JAKOVLJEVIĆ, S. 1928.
Contributions à la connaissance de la structure et de la fonction des poils.
Bull. Inst. Jard. Bot. Univ. Belgrade 1: 14-32.

JEPSON, W.L. 1943.
A Flora of California. Vol. 3. Berkeley, California: Associated Students Store, University of California at Berkeley.

*JERMANOWSKA, Z.& SYKULSKA, Z. 1964.
Chem. Abstr. 61: 6438-b.

JODIN, H. 1903.
Recherches anatomiques sur les borraginées.
Ann. Sci. Nat. Bot. ser. 7, 17: 263-346.

JOHNSTON, I.M. 1923.
Studies in the Boraginaceae 2. The genus Antiphytum.
Contr. Gray Herb. Harvard Univ. 68: 48-52.

JOHNSTON, I.M. 1924a.
Studies in the Boraginaceae 2 (sic). American native and immigrant borages of the Boraginoideae.
Contr. Gray Herb. Harvard Univ. 70: 1-61.

JOHNSTON, I.M. 1924b.
Studies in the Boraginaceae 3. The Old World genera of the Boraginoideae.
Contr. Gray Herb. Harvard Univ. 73: 42-73.

JOHNSTON, I.M. 1927.
Studies in the Boraginaceae 6. A revision of the South American Boraginoideae.
Contr. Gray Herb. Harvard Univ. 78: 3-118.

JOHNSTON, I.M. 1935.
Studies in the Boraginaceae 11 (3). New or otherwise noteworthy species.
J. Arn. Arb. 16: 174-205.

JOHNSTON, I.M. 1937a.
Studies in the Boraginaceae 12 (1). Trigonotis in southwestern China.
J. Arn. Arb. 18: 1-10.

JOHNSTON, I.M. 1937b.
Studies in the Boraginaceae 12 (2). Novelties and critical notes.
J. Arn. Arb. 18: 10-25.

JOHNSTON, I.M. 1940.
Studies in the Boraginaceae 14. Miscellaneous species from Asia, Malaysia and America.
J. Arn. Arb. 21: 48-66.

JOHNSTON, I.M. 1951.
Studies in the Boraginaceae 21. Sino-Indian species of Onosma.
J. Arn. Arb. 32: 201-225, 344-368.

JOHNSTON, I.M. 1952.
Studies in the Boraginaceae 23. A survey of the genus Lithospermum.
J. Arn. Arb. 33: 299-366.

JOHNSTON, I.M. 1953a.
Studies in the Boraginaceae 24. A. Three genera segregated from Lithospermum. (pp. 1-6). B. Supplementary notes on Lithospermum. (pp. 7-16).
J. Arn. Arb. 34: 1-16.

JOHNSTON, I.M. 1953b.
Studies in the Boraginaceae 25. A revaluation of some genera of the Lithospermeae.
J. Arn. Arb. 34: 258-299.

JOHNSTON, I.M. 1954a.
Studies in the Boraginaceae 26. Further revaluations of the genera of the Lithospermeae.
J. Arn. Arb. 35: 1-81.

JOHNSTON, I.M. 1954b.
Studies in the Boraginaceae 27. Some general observations concerning the Lithospermeae.
J. Arn. Arb. 35: 158-166.

JOHNSTON, I.M. 1957.
Studies in the Boraginaceae 29. Echiochilon and related genera.
J. Arn. Arb. 38: 255-293.

JONOVÁ, Maruška 1927.
Anatomie a morfologie trichomů u Borraginacei s ohledem na systematiku této čeledi.
Vestník Královské České Společnosti Nauk 1926: Art. 18 (66 pp.).

*JUZEPČUK, S.V. 1958.
(The Komarovian conception of the species, its historical development and expression in the flora U.R.S.S.).
Akad. Nauk. S.S.S.R., Bot. Inst. V.I. Komarova 1958 (1): 130-204 (transl).

KAZMI, S.M.A. 1970-1971.
A revision of the Boraginaceae of West Pakistan and Kashmir.
1. (Family description, key to genera, Cordia, Ehretia, Coldenia, Heliotropium, Sericostoma, Bothriospermum, Echiochilon): J. Arn. Arb. 51: 183-184 (1970).
2. (Lasiocaryum, Pseudomertensia, Anoplocaryum, Eritrichium, Hackelia, Microula, Trigonotis): J. Arn. Arb. 51: 367-402 (1970).
3. (Lappula, Lepechiniella, Heterocaryum): J. Arn. Arb. 51: 499-520 (1970).
4. (Rochelia, Asperugo, Omphaloden, Paracaryum, Mattiastrum, Solenanthus): J. Arn. Arb. 52: 110-136 (1971).
5. (Arnebia, Onosma, Trichodesma): J. Arn. Arb. 52: 486-522 (1971).
6. (Caccinia, Anchusa, Nonea, Decalepidanthus, Gastrocotyle, Myosotis): J. Arn. Arb. 52: 666-690 (1971).

KAZMI, S.M.A. 1975.
Ivanjohnstonia jaunsariensis - a new genus and species of Boraginaceae from Northwest Himalayas.
Sultania 1: 1-4.

*KOLCHANOV, A.F. 1972a.
Dannye geografii k sistematike podsemeistua Rosoideae Focke (Geographic data applied to the taxonomy of the subfamily Rosoideae Focke).
Zap. Tsentr.-Kavkaz Otd. Vses. Bot. O-VA. 3: 85-87. (Translated from Ref. Zh. Biol. 1972, 12V541).

*KOLCHANOV, A.F. 1972b.
Palinologicheskie dannye k obosnovaniyu novoi sistemy podsemeistua rozovlych (Palynological data for substantiating the new taxonomic system of the subfamily Rosoideae).
Zap. Tsentr.-Kavkaz Otd. Vses. Bot. O-VA 3: 93-94. (Translated from Ref. Zh. Biol. 1972, 12V543).

KUNZE, G. 1850.
Borraginearum novum genus proposuit G. Kunze: Trachelanthus Kze.
Bot. Zeitung. 8: 665.

KUSNETZOV, N.I. 1910.
Sistematika roda Rindera Pall. (Systematics of the genus Rindera Pall.).
Trav. Mus. Bot. Acad. St Petersb. 7: 20-70.

KUSNETZOV, N.I. 1913.
Boraginaceae, in KUSNETZOV, N.I., BUSH, N. & FOMIN, A.
Flora Caucasia Critica 4 (2): 66-400. Leningrad.

*KUYL, O.S., MULLER, J. & WATERBOLK, H.T. 1955.
The application of palynology to oil geology with reference to western Venezuela.
Geol. Mijnbouw 17: 49-76.

LALL, S.S. 1970 (unpubl.).
Taxonomic Studies in the Genus Scrophularia.
Ph.D. Thesis, University of Edinburgh.

LAMARCK, J.B.A.P.M. de 1786.
Encyclopédie Méthodique. Botanique. vol. 2. Paris: Panckoucka, Agasse.

LAWRENCE, Julia R. 1937.
A correlation of the taxonomy and floral anatomy of certain Boraginaceae.
Amer. J. Bot. 24: 433-444.

*LAZAREV, A.V. 1972.
K sistematike sem. Lobeliaceae (Taxonomy of the family Lobeliaceae).
Zap. Tsentr.-Kavkaz Otd. Vses. Bot. O-VA 3: 101-104. (Translated from Ref. Zh. Biol. 1972, 12V588).

LEDEBOUR, C.F. von 1829a.
Icones plantarum novarum vel imperfecte cognitarum, Florum Rossicam, imprimis altaicam, illustrantes.
Riga: I. Deubner.

LEDEBOUR, C.F. von 1829b.
Flora Altaica. Berlin: Reimer.

LEHMANN, J.G.C. 1818.
Plantae e familia Asperifoliarum nuciferae. Berlin: Dammler.

LEHMANN, J.G.C. 1851.
Lindelofia (Novum Genus Borraginearum, e subordine Cynoglossearum).
In Indices Seminum (anno) 1850, 7.- Index Hortus Hamburgensis.
Linnaea 24: 215-216.

LEMÉE, A. 1929-41.
Dictionnaire descriptif et synonymique des genres de plantes phanérogames.
Brest: Imp. Commerciale et Admin.

LEMS, K. & HOLZAPFEL, C.M. 1968.
Evolution in the Canary Islands. 1. Phylogenetic relations in the genus Echium (Boraginaceae) as shown by trichome development.
Bot. Gaz. 129: 95-107.

LÉVEILLÉ, A.A.H. 1913.
Decades plantarum novarum CXII-CXVIII.
Feddes Rep. 12: 181-191.

LEVEQUE, M. & GORENFLOT, R. 1969.
Prospections caryologues dans la flore littorale du Boulonnais.
Bull. Soc. Bot. Nord.France 22: 27-58.

LEVIN, D.A. & YORK, B.M. 1978.
The Toxicity of Plant Alkaloids: an ecogeographic perspective.
Biochem. Syst. Ecol. 6: 61-76.

LEWIS, H. 1972.
The origin of endemics in the California flora.
In VALENTINE, D.H. (ed.), Taxonomy, Phytogeography and Evolution pp. 179-189. London and New York: Academic Press.

LINCHEVSKY, A. & PROZOROVSKY, A.V. 1949.
The basic principles of the distribution of the vegetation of Afghanistan.
Kew Bull. 1949: 179-214.

LINNAEUS, C. 1742.
Genera Plantarum ed. 2. Leiden.

LINNAEUS, C. 1753.
Species Plantarum ed. 1. Stockholm.

LINNAEUS, C. 1762.
Species Plantarum ed. 2. Stockholm.

LINNAEUS, C. 1764.
Species Plantarum ed. 3. Wien.

LIPSKY, V.I. 1904.
Flora Asiae Mediae seu Turkestaniae Rossicae inclusis chanatis Buchara et Chiwa.
Petropoli: Herold.

LITARDIÈRE, R. de 1941.
Recherches caryologiques et caryotaxonomiques sur les Boraginacées.
Bull. Soc. Hist. Nat. Afrique Nord 32: 315-330.

van LOON, J. Chr. & de JONG, H. 1978.
(Chromosome number report for Cynoglossum columnae).
In LÖVE, A. (ed.) IOPB chromosome number reports LIX.
Taxon 27: 53-61.

LÖVE, A. & LÖVE, Doris 1956.
Cytotaxonomical conspectus of Icelandic flora.
Acta Hort. Gotob. 20: 65-290.

MACBRIDE, J.F. 1916.
Contributions from the Gray Herbarium of Harvard University, new series no. 45. Part 3: Certain Boraginaceae new or transferred.
Proc. Amer. Acad. Arts & Sci. 31: 541-548.

MAHESHWARI, P. 1950.
An introduction to the embryology of angiosperms. New York: McGraw Hill.

MAIRE, R. 1921.
Contributions à l'étude de la flore de l'Afrique du Nord, 2.
Bull. Soc. Hist. Nat. Afrique Nord 12: 42-52.

MAIRE, R. 1936.
Contributions à l'étude de la flore de l'Afrique du Nord, 24.
Bull. Soc. Hist. Nat. Afrique Nord 27: 203-233.

MÁJOVSKÝ, J. 1970.
Index to chromosome numbers of Slovakian flora 1.
Acta Fac. Rerum Nat. Univ. Comenianae Bot. 16: 1-26.

MÁJOVSKÝ, J. et al. 1974.
Index of chromosome numbers of Slovakian flora 4.
Acta Fac. Rerum Nat. Univ. Comenianae Bot. 23: 1-23.

*MAŇKO, I.V. 1966.
Chem. Abstr. 64: 4125b.

*MAŇKO, I.V. 1972.
Izvehenie alkaloidov Cynoglossum amabile Stapf et Drumm. & C. viridiflorum Pall. ex Lehm.
Rast. Resur. 8: 243-246.

*MAŇKO, I.V. & MARCHENKO, L.G. 1972a.
Izvehenie alkaloidov Cynoglossum pictum.
Khim. Prir. Soedin (Tashk.) 7: 676-677.

*MAŇKO, I.V. & MARCHENKO, L.G. 1972b.
Piktumin - - novye alkaloid iz Cynoglossum pictum.
Khim. Prir. Soedin (Tashk.) 8: 655-656.

*MAŇKO, I.V. & MARCHENKO L.G. 1972c.
Alkaloidy kornei Cynoglossum pictum.
Khim. Prir. Soedin (Tashk.) 8: unpag.

*MAŇKO, I.V. & VASIL'KOV, P.N. 1968.
/Lappula intermedia alkaloids/.
Tr. Leningrad Khim.-Farm. Inst. 26: 166-173
(as cited in Chem. Abstr. 73: 73849, 1970).

*MANNING, A. 1956.
Some aspects of the foraging behaviour of bumble-bees.
Behaviour 9: 164-201.

MANSKE, R.H.E. & HOLMES, H.L. 1960.
The Alkaloids, Chemistry and Physiology. London & New York: Academic Press.

*MARKOWA, M. & IVANOVA, P. 1966.
Karyologische Untersuchungen der Vertreter der Fam.-Borraginaceae, Labiatae und Scrophulariaceae in Bulgarien, 2.
Izv. Bot. Inst. Bulg. Akad. Nauk Otd. Biol. Nauki 21: 123-131.

MARTICORENA, C. 1968.
Granos de polen de plantas chilenas: I.
Gayana Bot. 17: 1-66.

MASAMUNE, G. 1930.
Contribution to our knowledge of the flora of the southern part of Japan.
J. Soc. Trop. Agric. Taiwan 2: 240-241.

MATHEZ, J. 1976 ('1975').
Contribution de la palynomorphologie à la connaissance des Cynoglossées du Bassin Méditerranéen Occidental.
In La Flore de Bassin Méditerranéen-Essai de Systématique Synthétique, pp. 279-287. Paris: Éditions du CNRS, Centre National de la Recherche Scientifique.

MAXIMOWICZ, C.J. 1872.
Borraginaceae Sino-Japonicae, in Diagnoses plantarum novarum asiaticarum Decas II.

MAXIMOWICZ, C.J. 1880.
Diagnoses plantarum novarum asiaticarum 3.
Mélanges Biologiques 10(3): 567-741 / Bull. Acad. Imp. Sci. St. Petersb. 26: 420-542.

MAXIMOWICZ, C.J. 1881.
Diagnoses plantarum novarum asiaticarum 4.
Mélanges Biologiques 11(9): 155-350 / Bull. Acad. Imp. Sci. St. Petersb. 27: 445-560.

MELCHIOR, H. 1939.
Neue Arten von Nanga Parbat leg. C. Troll.
Notizbl. Bot. Gart. Mus. Berlin-Dahlem 14(124): 342-355.

MERXMÜLLER, H. 1972.
Systematic botany: an unachieved synthesis.
Biol. J. Linn. Soc. 4: 311-321.

MERXMÜLLER, H. & GRAU, J. 1963.
Chromosomenzahlen aus der Gattung Myosotis L.
Ber. Deuts. Bot. Ges. 76: 23-29.

MERXMÜLLER, H. & GRAU, J. 1969.
Dysploide bei Pulmonaria.
Rev. Roum. Biol. Ser. Bot. 14: 57-63.

METCALFE, J.R. & CHALK, L. 1950.
Anatomy of the Dicotyledons, 2. Oxford: Clarendon Press.

MIGO, H. 1942.
New or noteworthy plants from China 1.
Bot. Mag. Tokyo 56: 265-270.

MILL, R.R. 1977a.
Solenanthus, in DAVIS, P.H. (ed.), Materials for a Flora of Turkey XXXIV.
Notes R.B.G. Edinb. 35: 308.

MILL, R.R. 1977b.
Paracaryum, in DAVIS, P.H. (ed.), Materials for a Flora of Turkey XXXIV.
Notes R.B.G. Edinb. 35: 303-308.

MILL, R.R. 1977c.
Trachelanthus, in DAVIS, P.H. (ed.), Materials for a Flora of Turkey XXXIV.
Notes R.B.G. Edinb. 35: 309-310.

MILL, R.R. 1979a.
Rindera, in DAVIS, P.H. (ed.), Flora of Turkey 6: 300-303.

MILL, R.R. 1979b.
Trachelanthus, in DAVIS P.H. (ed.), Flora of Turkey 6: 305-306.

MILL, R.R. 1979c.
Solenanthus, in DAVIS, P.H. (ed.), Flora of Turkey 6: 303-305.

MILL, R.R. 1979d.
Paracaryum, in DAVIS, P.H. (ed.), Flora of Turkey 6: 282-300.

MILLER, P. 1752.
The Gardener's Dictionary ed. 6. London: The author.

MILLER, P. 1754.
The Gardener's Dictionary abridged from the folio edition ed. 4.
London: J. & J. Rivington.

MILLSAPS, Vera 1940.
Structure and development of the seed of Cynoglossum amabile Stapf & Drumm.
J. Elisha Mitchell Sci. Soc. 56: 140-164.

MOENCH, C. 1794.
Methodus plantas horti botanici et agri marburgensis.
Marburg: Cathorum in Officina nova libraria academiae.

MOHL, H. von 1835.
Sur la structure et les formes des graines de pollen.
Ann. Sci. Nat. Bot. ser. 2, 3: 148-180, 220-236, 304-346.

MORA, D. Mariano del Amo y 1872.
Flora fanerogamica de la Peninsula Iberica. Vol. 3: Coroliflorae.
Granada: De Indalecio Ventura.

MOUTERDE, P. (ed. CHARPIN, P. & GREUTER, W.) 1978.
Nouvelle flore du Liban et de la Syrie. Part 3, fasc. 1.
Beirut: Dar El-Machreq Editeurs.

MULLIGAN, G.L. 1957.
Chromosome numbers in Canadian weeds 1.
Can. J. Bot. 35: 779-789.

MUNZ, P.A. & KECK, D.D. 1959.
A California flora. Berkeley: University of California Press.

MURBECK, S. 1898.
Contributions à la connaissance de la Flore du Nord-Ouest de l'Afrique et plus specialement de la Tunisie. Lund: Malmström.

MURBECK, S. 1922.
Contributions à la connaissance de la Flore du Maroc, 1: II, 2. Geraniacées-Composées.
Lunds Univ. Årsskr. N.F. avd. 2 Bd. 19 Nr. 1 (Kungl. Fysiograf. Sällskapets Handl. N.F. Bd. 34 Nr. 1). (Boraginaceae: pp. 19-23).

MURIN, A. & SHEIKH, M.Y. 1971.
(Chromosome number report for Heliotropium suavolens M.B.).
In LÖVE, A. (ed.), IOPB Chromosome Number Rept. 32. Taxon 20: 353.

*MURIN, V. 1967.
Islov. fl. I.

*NAGARAJ, M. & FATHIMA, Tasneem 1968.
A note on the sporogenesis and gametogenesis in Adelocaryum.
Curr. Sci. 37: 265-267.

NAKAI, T. 1923.
Notulae ad plantas Japoniae et Koreae 29.
Bot. Mag. Tokyo 37: 1-17.

NILSSON, Ö. 1967.
Studies in Montia L., Claytonia L. and allied genera III.
Pollen morphology.
Grana Palynol. 7: 280-363.

NOWICKE, Joan W. 1968.
Palynotaxonomic study of the Phytolaccaceae.
Ann. Missouri Bot. Gard. 55: 294-364.

NOWICKE, Joan W. 1970.
Pollen morphology in the Nyctaginaceae.
Grana 10: 79-87.

NOWICKE, Joan W. & RIDGWAY, J.E. 1973.
Pollen studies in the genus Cordia (Boraginaceae).
Amer. J. Bot. 60: 584-591.

NOWICKE, Joan W. & SKVARLA, J.J. 1974.
A palynological investigation of the genus Tournefortia (Boraginaceae).
Amer. J. Bot. 61: 1021-1036.

OHWI, J. 1956a.
Notes on some plants from Japan and its neighbours.
Bull. Nat. Sci. Mus. Tokyo 3: 98-101.

OHWI, J. 1956b.
Flora of Japan. Shibundo, Tokyo.

*PAL, P.K. 1957.
Chromosome number in the genus Heliotropium Linn.
Curr. Sci. 26: 218.

*PAL, P.K. 1963.
Comparative studies in 4 species of Heliotropium L.
Proc. Nat. Inst. Sci. India B 29: 1-41.

PALLAS, P.S. 1771.
Reise durch verschiedene Provinzen des russischen Reichs. St. Petersburg.

PALSER, Barbara F. 1976 ('1975').
The Bases of Angiosperm Phylogeny: Embryology.
Ann. Missouri Bot. Gard. 62: 621-646.

PAVLOV, N.V. 1964.
Flora Kazakhstana vol. 7. Alma Ata. Akademiya Nauk Kazakhskoi SSR., Institut Botaniki.

PAWŁOWSKI, B. 1962.
Annotationes de Pulmonaria.
Acta Soc. Bot. Poloniae 31: 229-238.

PAZIJ, T. 1959.
Bot. Mat. Herb. Inst. Bot. Akad. Uzbek. SSR 15: 24-29.

PITARD, C.-J. 1918.
Contribution à l'étude de la flore du Maroc. ed. 1. Tours: mimeographed holograph text.

PITARD, C.-J. 1931 (posth.)
Contribution à l'étude de la flore du Maroc. ed. 2. Gap.

PLOUVIER, V. 1958.
Sur la recherche du bornésitol chez les Rhamnacées, Boraginacées et quelques autres familles.
Compt. Rend. Acad. Sci. Paris 247: 2190.

PLOUVIER, V. 1971a.
Sur la recherche du scyllitol, du myo-inositol et du dulcitol dans quelques groupes botaniques.
Compt. Rend. Acad. Sci. Paris 272D: 141-144.

PLOUVIER, V. 1971b.
Nouvelle recherche du scyllitol dans quelques groupes botaniques: sa large répartition chez les Composées.
Compt. Rend. Acad. Sci. Paris 273D: 1625-1628.

PODLECH, D. & BADER, O. 1974.
Chromosomen Studien an afghanischen Pflanzen II.
Mitt. Bot. Staatssamml. München 11: 457-488.

PONERT, J. 1977.
Ergasiophygophytes and Xenophytes of East Asiatic origin in Adjaria: A stimulus to new terminology, especially for Ergasiophygophytes.
Folia Geobot. Phytotax. (Praha) 12: 9-22.

POPE, M.A. 1925.
Pollen grain morphology as an index to plant relationship.
Bot. Gaz. 80: 66.

POPOV, M.G. 1916.
In Karowin, E.P., Kultiasov, M.W. & Popov, M.G. Descriptiones plantarum in Turkestania lectarum.
In N.A. DIMO, Pochv. i bot. issl. v bass. r.r. Syr-Dar'i i Amu-Dar'i i 2: 64.

POPOV, M.G. 1950.
De genere Rinderae florae URSS.
Not. Syst. (Leningrad) 13: 212-227.

POPOV, M.G. 1951.
Boraginaceae novae.
Not. Syst. (Leningrad) 14: 305-335.

POPOV, M.G. 1953.
Boraginaceae. In SHISKIN (ed.), Flora URSS 19: 97-691. (Translated by Israel Program for Scientific Translations, Jerusalem, 1974).

POST, G.E. 1896.
Flora of Syria, Palestine and Sinai from the Taurus to Ras Muhammad and from the Mediterranean Sea to the Syrian Desert. ed. 1.
Beirut: Syrian Protestant College.

POST, G.E. ed. DINSMORE, J.E. 1932.
Flora of Syria, Palestine and Sinai. ed. 2. Beirut: Publ. Fac. Arts & Sciences, American University of Beirut.

PROCTOR, M. & YEO, P. 1973.
The Pollination of Flowers. London: Collins (The New Naturalist).

RAFFAUF, R.F. 1970.
A Handbook of alkaloids and alkaloid - containing plants.
New York: Wiley.

RAU, M.A. 1975.
High Altitude Flowering Plants of West Himalayas.
Howrah: Botanical Survey of India.

RAVEN, P.H. 1976 ('1975').
The Bases of Angiosperm Phylogeny: Cytology.
Ann. Missouri Bot. Gard. 62: 724-764.

RAVEN, P.H. & AXELROD, D.I. 1978.
Origins and Relationships of the California Flora. University of California Publications in Botany 72. 134 pp. Berkeley, Los Angeles & London: University of California Press.

RAVEN, P.H., KYHOS, D.W. & HILL, A.J. 1965.
Chromosome numbers of spermatophytes, mostly Californian.
Aliso 6: 105-113.

RAY, P.M. 1954.
Cytological, genetic, morphological study of evolution in the borage genus Amsinckia.
VIII Congr. Internatl. Bot., Rapp. et Comm. parvenus avant le Congrès sect. 9 et 10: 188-190.

RAY, P.M. & CHISAKI, H.F. 1957a.
Studies on Amsinckia 2. Relationships among the primitive species.
Amer. J. Bot. 44: 537-544.

RAY, P.M. & CHISAKI, H.F. 1957b.
Studies on Amsinckia 3. Aneuploid diversification within the Muricatae.
Amer. J. Bot. 44: 545-554.

RECHINGER, K.H. fil. 1947.
Plantae novae orientales.
Ann. Naturh. Mus. Wien 55: 5-18.

RECHINGER, K.H. fil. 1949.
Beschreibungen neuer orientalischen Pflanzenarten.
Svensk Bot. Tidskr. 43: 37-45.

RECHINGER, K.H. fil. 1951.
Boraginaceae novae orientales (Rechingeri iter iranicum secundum No. 24).
Ann. Naturh. Mus. Wien 58: 44-61.

REGEL, E. 1878.
Descriptiones plantarum novarum et minus cognitarum fasc. 6. B. Plantae Turkestanicae a Regelio et Smirnowio determinatae.
Acta Horti Petrop. 5: 621-626.

REGEL, E. 1882.
Descriptiones plantarum novarum rariorumque a cl. Olga Fedtschenko in Turkestania nec non in Kokania lectarum. 89 pp. St. Petersburg.
(Also published in Denkschr. Ges. Nat. Anthrop. Ethnogr. Moskau 34 (2)).

REICHENBACH, H.G. 1857.
Icones florae Germanicae et Helveticae. Vol. 18. Leipzig: Hofmeister.

REINBOTHE, H. 1961.
Zur Frage der Biosynthese von Allantoin und Allantoinsäure in höheren Pflanzen.
Flora 150: 128-165.

REITSMA, T. 1970a.
Suggestions towards unification of descriptive terminology of angiosperm pollen grains.
Rev. Palaeobot. Palynol. 10: 39-60.

REITSMA, T. 1970b.
Pollen morphology of the Alangiaceae.
Rev. Palaeobot. Palynol. 10: 249-332.

REVEDIN, P. 1902.
Studio sopra i pelli dello Borraginacee.
Nuovo Gior. Bot. Ital. n.s. 9: 301-318.

RICKETT, H.W. 1966.
Wild Flowers of the United States. 1. The Northeastern States.
New York: McGraw Hill.

RIEDL, H. 1962.
Bemerkungen über Cynoglossum coelestinum Lindl. und C. glochidiatum Wall. sowie Versuch einer Neugliederung der Gattung Cynoglossum L.
Öst. Bot. Zeitschr. 109: 385-394.

RIEDL, H. 1963a.
Bemerkungen über oder kritische Borraginaceen der Asiatischen Flora.
Öst. Bot. Zeitschr. 110: 511-542.

RIEDL, H. 1963b.
Boraginaceae. In KØIE, M. & RECHINGER, K.H. fil., Symbolae Afghanicae V.
Dansk. Biol. Skrift. 13: 183-252.

RIEDL, H. 1967.
Boraginaceae. In K.H. RECHINGER fil. (ed.), Flora Iranica 48.
Graz: Akademische Druck- u. Verlagsantalt. 281 pp.

RIEDL, H. 1968.
Die neue Tribus Trigonotideae und das System der Boraginoideae.
Öst. Bot. Zeitschr. 115: 291-321.

RIEDL, H. 1969.
Über zwei verkannte Paracaryum-Arten der UdSSR.
Öst. Akad. Wiss. Mat. Naturw. Kl. Anz. 106(1-14): 6-12.

RIEDL, H. 1971.
Die Gattung Adelocaryum Brand.
Öst. Bot. Zeitschr. 119: 168-173.

RIEDL, H. 1972.
Solenanthus micranthus H. Riedl, eine neue Boraginaceen-Art aus Afghanistan.
Ann. Naturh. Mus. Wien 76: 635-638.

RIEDL, H. 1979 ('1978').
Cynoglossum. In DAVIS (ed.), Flora of Turkey and the East Aegean Islands 6: 306-311.

RIEDL, H. & FREITAG, H. 1972.
Drei neue Boraginaceen-Species der Flora von Afghanistan.
Öst. Bot. Zeitschr. 120: 137-142.

ROBINSON, B.C. 1891.
Descriptions of new plants, chiefly Gamopetalae, collected in Mexico by C.C. Pringle in 1889 and 1890.
Proc. Amer. Acad. Arts & Sci. 26: 164-176.

ROBYNS, W. 1948-1955.
Flore des spermatophytes de Parc National Albert. Brussels: Institute des Parcs National du Congo Belge.

ROEMER, J.J. & SCHULTES, J.A. 1819.
Caroli Linné equitis Systema Vegetabilium ... Editio nova, speciebus inde ab editione XV detectis aucta et locupleta. Stuttgart: J.G. Cotta.

ROLAND, A.E. & SMITH, E.C. 1969.
The Flora of Nova Scotia. Part II: The Dicotyledons.
Proc. Nova Scotia Inst. Sci. 26: 277-743.

ROLLINS, R.C. 1965.
On the bases of biological classification.
Taxon 14: 1-6.

RYDBERG, P.A. 1922.
Flora of the Rocky Mountains and adjacent plains. xii + 1110.(-1144 incl. Appendix). New York: privately published.

SAUER, W. 1970.
Pulmonaria in Oberösterreich.
Mitt. Bot. Arbeitsgem. Oberösterr. Landesmus. Linz 2: 47-48.

SAUER, W. 1972.
Die Gattung Pulmonaria in Oberösterreich.
Öst. Bot. Zeitschr. 120: 33-50.

SAUER, W. 1973.
Beitrag zur Kenntnis von Pulmonaria stiriaca Kerner und Verwandten (Boraginaceae).
Mitt. Bot. München 11: 1-31.

SAUER, W. 1974.
Beitrag zur Kenntnis von Pulmonaria montana Lejeune und P. mollis Wulfen (recte: Wolff) ex Hornemann in Mitteleuropa.
Phyton (Austria) 16: 239-264.

SAUER, W. 1975.
Karyosystematische Untersuchungen an der Gattung Pulmonaria (Boraginaceae).
Bibl. Bot. 131: (85 pp.).

SAUVAGE, C. 1961.
Flore des subéraies Marocaines.
Trav. Inst. Sci. Chérifien sér. Bot. 22: xvi + 252 pp.

SAUVAGE, C. & VINDT, J. 1954.
Flore du Maroc: Analytique, Descriptive et Illustré. Fasc. II.
Spermatophytes (Tubiflorales - Convolvulacées et Boraginacées).
Trav. Inst. Sci. Chérifien sér. Bot. 3: fasc. 11.

*SCHACHT, H. 1860.
Über den Bau einiger Pollenkorner.
Pringsheim's Jahrb. 2: 109-168.

SCHREBER, J.C.D. von 1789.
Caroli a Linné, Genera Plantarum ed. 8. Francofurti ad Moenum: Varrentrappii et Wenneri.

SCHULTES, J.A. 1809.
Observationes Botanicae in Linnaei Species Plantarum ex C.L. Willdenow.
Oenoponti.

SCHURHOFF, P.N. 1926.
Die Zytologie der Blütenpflanzen. Stuttgart: Verlag von Ferdinand Enke.

SCOGGAN, H.J. 1950.
The Flora of Bic and the Gaspé Peninsula, Quebec.
National Museum of Canada Bull. 115 (Biol. ser. no. 39). Ottawa:Dept. of Resources and Development, Development Services Branch.

SHMIDA, A. 1978.
Relationships between Paracaryum intermedium and P. boissieri on Sinai, and the generic separation of Paracaryum and Mattiastrum (Boraginaceae).
Plant Syst. Evol. 129: 323-326.

SHREVE, F. & WIGGINS, I.C. 1964.
Vegetation and Flora of the Sonoran Desert. Stanford: University Press.

SINGH, T.C.N. 1931.
Studies in the morphology of pollen grain. 1(a) Boraginaceae.
J. Ind. Bot. Soc. 10: 38-42.

*SKALINSKA, M., CZAPIK, R., PIOTROWICZ, M. et al. 1959.
(Further notes in chromosome numbers of Polish Angiosperms (Dicotyledons))
Acta Polsk. Towarz. Bot. 28: 487-529.

SMALL, J.K. 1903.
Flora of the Southeastern United States. New York: privately published.

SMITH, A.C. 1969.
Systematics and Appreciation of Reality.
Taxon 18: 5-13.

SMITH, E.B. 1966.
(Chromosome number report for Heliotropium convolvulaceum Gray).
In LÖVE, A. (ed.), IOPB Chromosome Number Rept. 7. Taxon 15: 155-163.

SOLEREDER, H. 1908. (Translated by L.A. BOODLE & F.E. FRITSCH; revised by D.H. SCOTT).
Systematic anatomy of the dicotyledons; a handbook for laboratories of pure and applied botany. Oxford: Clarendon Press.

SOUÈGES, R. 1938a.
Embryogénie des Boragacées. Développement de l'embryon chez le Lycopsis arvensis L.
Compt. Rend. Acad. Sci. Paris 207: 640-642.

SOUÈGES, R. 1938b.
Embryogénie des Boragacées. Développement de l'embryon chez l'Echium vulgare L.
Compt. Rend. Acad. Sci. Paris 212: 871-872.

SOUÈGES, R. 1941.
Embryogénie des Boragacées. Développement de l'embryon chez le Symphytum officinale L.
Compt. Rend. Acad. Sci. Paris 212: 245-246.

SOUÈGES, R. 1958.
Embryogénie des Boragacées. Développement de l'embryon chez Omphalodes linifera Moench (sic).
Compt. Rend. Acad. Sci. Paris 247: 249-253.

STAFLEU, F. 1961.
Boraginaceae. In S.J. van OOSTSTROOM & T.J. REICHGELT (eds.), Flora Neerlandica 4(1): 92-140.

et al.
STAFLEU, F.A./(ed.) 1978.
International Code of Botanical Nomenclature, adopted by the twelfth International Botanical Congress, Leningrad, July 1975.
Regnum Vegetabile 98. Utrecht: Bohn, Holkema & Scheltema.

STEBBINS, G.L. 1969.
Comments on the search for a 'perfect system'.
Taxon 18: 357-359.

STEBBINS, G.L. 1971.
Chromosomal evolution in higher plants. London: Edward Arnold (Publishers) Ltd.

STEBBINS, G.L. 1974.
Flowering Plants. Evolution above the species level. Cambridge (Mass.): The Belknap Press of Harvard University Press.

STIX, Erika 1964.
Pollenmorphologie von Borago officinalis L.
Grana Palynol. 5: 24-32.

*STREY, M. 1931.
Karyologische Studien an Borraginoideae.
Zeitschr. Wiss. Biol. Abt. E, Planta 14(3/4): 682-730.

STRID, A. 1971.
Chromosome numbers in some Albanian angiosperms.
Bot. Not. 124: 490-496.

SUBRAMANYAM, K. & KAMBLE, N.P. 1967.
(Chromosome number report for Heliotropium curassavicum L.).
In LÖVE, A. (ed.), IOPB Chromosome Number Rept. 12. Taxon 16: 349.

SUGIURA, T. 1940a.
Studies on the chromosome numbers of higher plants 5.
Cytologia 10: 363-370.

*SUGIURA, T. 1940b.
A list of chromosome numbers in angiospermous plants.
Proc. Imp. Acad. Tokyo 16: 15-16.

SVENSSON, H.G. 1925.
Zur Embryologie der Hydrophyllaceen, Borraginaceen und Heliotropaceen mit besonderer Rücksicht auf die Endospermbildung. Inaugural Dissertation, Uppsala.

SWEET, R. 1827.
Sweet's Hortus Britannicus. London: J. Ridgway.

SYSTEMATICS ASSOCIATION COMMITTEE FOR DESCRIPTIVE BIOLOGICAL TERMINOLOGY (SADT) 1962.
Terminology of simple symmetrical plane shapes.
Taxon 11: 145-156.

TAKHTAJAN, A. 1969.
Flowering Plants: Origin and Dispersal. London & Edinburgh: Oliver & Boyd.

TARNAVSCHI, T. & RADULESCU, D. 1960.
Cercetări morfologice asupra microsporilor de Boraginaceae din Flora R.P. Rômine.
Stud. Cercet. Biol. (Bucharest): 12: 73-93.

TÉTÉNYI, P. 1974.
Données chimiotaxinomiques sur les Boraginacées.
Acta Bot. Acad. Sci. Hung. 20: 159-167.

THORNE, R.F. 1976.
A phylogenetic classification of the Angiospermae.
In M.K. HECHT, W.C. STEERE & B. WALLACE (eds.), Evolutionary Biology 9: 35-106. London & New York: Plenum Press.

van TIEGHEM, P. 1907.
Structure du pistil et du fruit des Labiées, des Boragacées et des familles voisines.
Ann. Sci. Nat. Bot. ser. 9, 5: 321-350.

*TOMCZYK, Helena 1969.
Rozpowszechnienie alkaloidów pyrolizydynowych i ich znaczenie taksonomiczne wśród roślin wyższych. (Distribution of pyrrolizidine alkaloids and their taxonomic significance in higher plants).
Wiad. Bot. 13(3): 187-193.

TOURNEFORT, J.P. de 1700.
Institutiones rei herbariae. Editio altera. Paris.

TOURNEFORT, J.P. de 1703.
Corollarium. Paris.

TRAUSELD, W.R. 1969.
Wild flowers of the Natal Drakensberg. Cape Town: Purnell.

*TSERULNIKOVA, L.G., LABENSKII, A.S. & UTKIN, L.M. 1962.
J. Gen. Chem. USSR 32: 2663.

TURRILL, W.B. 1929.
On the flora of the Nearer East, 4.
Kew Bull. 1929: 223-235.

TUTIN, T.G. et al. 1964, 1968, 1972, 1976.
Flora Europaea.
Vol. 1. (Lycopodiaceae to Platanaceae) - 1964.
Vol. 2 (Rosaceae to Umbelliferae) - 1968.
Vol. 3 (Diapensiaceae to Myoporaceae) - 1972.
Vol. 4 (Plantaginaceae to Compositae, and Rubiaceae) - 1976.
Cambridge: University Press.

UHRIKOVÁ, A. & MÁJOVSKÝ, J. 1978.
(Chromosome number report for Omphalodes scorpioides).
In LÖVE, A. (ed.) IOPB chromosome number reports LXI.
Taxon 27: 375-392.

UPHOF, J.C.T. 1962.
Plant Hairs.
Handb. Pflanzenanatomie 4(5): 1-206.

VASUDEVAN, K.N. 1975.
Contribution to the Cytotaxonomy and Cytogeography of the Flora of the Western Himalayas (with an attempt to compare it with the Flora of the Alps). Part 1.
Bull. Soc. Bot. Suisse/Ber. Schweiz Bot. Ges. 85(1): 57-84.

VUILLEUMIER, Beryl S. 1967.
The origin and evolutionary development of heterostyly in the angiosperms.
Evolution 21: 210-226.

*WAGNER, H. & FRIEDRICH, H. 1964.
Über das Vorkommen einer Octadecatetraensäure in den Samen einigen Boraginaceen.
Naturwissenschaften 51: 164.

WALKER, J.W. & DOYLE, J.A. 1976 ('1975').
The Bases of Angiosperm Phylogeny: Palynology.
Ann. Missouri Bot. Gard. 62: 664-723.

WALTERS, S.M. 1965.
'Improvement' versus stability in botanical classification.
Taxon 14: 6-10.

WATSON, S. 1883.
Contributions to American Botany. 10(1). List of plants from Southwestern Texas and Northern Mexico, collected chiefly by Dr. E. Palmer in 1879-80. - II. Gamopetalae to Acotyledones.
Proc. Amer. Acad. Arts & Sci. 18: 96-191.

WATSON, S. 1890.
Contributions to American Botany. 17(2). Descriptions of New Species of Plants from Northern Mexico, collected chiefly by Mr C.G. Pringle, in 1888 and 1889.
Proc. Amer. Acad. Arts & Sci. 25: 141-163.

WERNHAM, H.F. 1911.
Floral evolution with particular reference to the sympetalous dicotyledons.
New Phytol. 10: 293-305.

WICKENS, G.E. 1969.
A revision of Symphytum L. in Turkey and adjacent areas.
Notes R.B.G. Edinb. 29: 157-180.

WILLIAMAN, J.J. & LI, Hui-Lin 1970.
Alkaloid-bearing plants and their contained alkaloids 1957-1968.
Lloydia 33 Suppl.: viii + 286.

WILLIAMAN, J.J. & SCHUBERT, B.G. 1961.
Alkaloid-bearing plants and their contained alkaloids.
Tech. Bull. 1234, Agric. Res. Service, U.S.D.A.

WILLDENOW, C.L. 1797.
Caroli a Linne Species plantarum ... Editio quarta, post Reichardianam quinta, adjectis vegetabilibus hucusque cognitis curante Carolo Ludovico Willdenow. Berlin.

WILLKOMM, M. & LANGE, J. 1870.
Prodromus florae hispanicae seu synopsis methodica omnium plantarum in Hispania sponte nascentium vel frequentius cultarum quae innotuerunt auctoribus. Vol. 2. Stuttgart: Schweizerbart.

ZAKIROV, A. 1941.
Burachnikouye Zeravshana (Boraginaceae of Seravschan).
Trudy Uzbek. Gos. Univ. 28.

*ZHUKOVA, P.G. 1967.
(Karyology of some plants cultivated in the Arctic-Alpine Botanical Garden).
In N.A. AVRORIN (ed.), Plantarum in Zonam Polarem Transportatio 2: 137-149. Leningrad.

ZOHARY, M. 1973.
Geobotanical foundations of the Middle East.
Stuttgart: Gustav Fischer Verlag.

INDEX

Names of genera accepted as belonging to Tribe Cynoglosseae as delimited in the present thesis are in BLOCK CAPITALS. Accepted species are in ordinary type; synonyms are underlined, and 'species dubiae' are indicated by broken underlining. For accepted taxa, and those excluded taxa treated in Chapter 28, the main text entry (that in the Systematic Treatment) is given first, followed by references to figures (ordinary type, in parentheses) and maps (underlined, in parentheses). Finally, subsidiary text references are listed in numerical order. For synonyms, and taxa not belonging to Tribe Cynoglosseae, all text references are arranged in numerical order.

D

E

L

R

S

U

V

Verbenaceae Jaume St.-Hil. 1, 2

Verbenales 1

W

Wellstediaceae(Pilger) Novak 1